Current limnological status of Owikeno Lake

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ABSTRACT

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Owikeno Lake was one of the major producers of sockeye salmon (*Oncorhynchus nerka*) in British Columbia (B.C.) until the late 1990's, when adult returns declined sharply. In 2001, we carried out a limnological study of Owikeno Lake to determine its current trophic status and to compare current limnological conditions with historical data to identify any changes that could have caused the recent decline in sockeye returns. Spring total phosphorus concentrations (3.4-5.4 µg/L), average chlorophyll concentrations (0.98-1.5 µg/L), average photosynthetic rates (113 mg $C \cdot m^{-2} \cdot d^{-1}$), sestonic C:N:P ratios (168:11:1), and a variety of other limnological variables all support the conclusion that Owikeno Lake is oligotrophic, but is more productive than most other coastal B.C. sockeye lakes. A sockeye rearing capacity model (the PR model) adjusted for conditions in Owikeno Lake predicts the lake currently has the capacity to produce 33 million smolts from a total escapement of 0.6 million. A comparison of limnological data (physical, chemical, and biological) from this study with data collected in various studies from the 1960's to the 1990's did not detect any changes in freshwater conditions that could be responsible for the recent declines in Owikeno sockeye. In the longer term, the commercial fishery reduced annual nutrient loading to the lake for much of the past century. Results from phosphorus loading models and anecdotal evidence from the early 1950's suggest that long-term declines in lake productivity have occurred as a result of this reduction. After assessing Owikeno Lake as a candidate for fertilization, we conclude that fertilization would possibly result in production increases which would benefit sockeye, but the probability of this occurring or of detecting those benefits is lower than in many other sockeye nursery lakes.

RÉSUMÉ

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Jusqu'à la fin des années 1990, le lac Owikeno a été l'une des grandes sources de saumon rouge (*Oncorhynchus nerka*) en Colombie-Britannique, puis les remontes d'adultes ont périclité. En 2001, nous avons réalisé une étude limnologique du lac Owikeno pour faire le point sur son état trophique et comparer les conditions limnologiques actuelles aux données historiques afin de repérer tout changement qui aurait pu expliquer la baisse récente des remontes de saumons rouges. Les concentrations totales de phosphore au printemps (3,4-5,4 µg/L), les concentrations moyennes de chlorophylle (0,98-1,5 µg/L), les taux moyens de la photosynthèse (113 mg C·m-2 d-1), les rapports C:N:P dans le seston (168:11:1) et une série d'autres variables limnologiques viennent confirmer que le lac Owikeno est oligotrophe, mais plus productif que la plupart des autres lacs côtiers de la Colombie-Britannique. Un modèle de la capacité de grossissement des saumons rouges (le modèle PR), ajusté en fonction des conditions qui règnent dans le lac Owikeno, prévoit que le lac a présentement la capacité de produire 33 millions de smolts à partir d'une échappée totale de 0,6 million de géniteurs. La comparaison des données limnologiques (physiques, chimiques et biologiques) de cette étude à des données recueillies au cours de diverses études menées des années 1960 aux années 1990 n'a fait ressortir aucun changement dans le milieu d'eau douce qui pourrait expliquer le déclin récent des saumons rouges du lac Owikeno. À grande échelle temporelle, la pêche commerciale a fait baisser la charge annuelle de matières nutritives du lac pendant la majeure

partie du siècle dernier. Les résultats des modèles de la charge de phosphore et les données anecdotiques du début des années 1950 permettent de penser que la baisse à long terme de la productivité du lac est liée à cette réduction. Après évaluation de l'intérêt du lac Owikeno comme candidat à la fertilisation, nous concluons qu'une fertilisation de ce lac pourrait se traduire par une hausse de la production qui serait favorable aux saumons rouges, mais que la probabilité de ce résultat ou de la détection de ces retombées est plus faible que dans de nombreux autres lacs d'alevinage du saumon rouge.

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INTRODUCTION

For most of the past 100 years, Owikeno Lake produced one of the larger runs of sockeye salmon in British Columbia. Although both catch and escapement varied, there were few distinct trends in abundance until the 1990's, when spawner numbers declined precipitously to a low of 3,600 in 1999 (Rutherford and Wood 2000). In both 2000 and 2001 spawner numbers increased slightly to approximately 20,000 (Holtby 2002), but were still far below the long-term historical average of 350,000. Possible causes of this decline could include changes in the freshwater environment and changes in marine conditions. Freshwater and marine survival indices for Owikeno sockeye indicate that the decline in stock size was attributable to marine and not freshwater conditions, but there is considerable uncertainty in some of the data used to calculate these indices (Rutherford et al. 1998; Rutherford and Wood 2000; McKinnell et al. 2001).

When reliable data are available, juvenile sockeye growth and survival rates (egg deposition to smolt numbers and biomass) provide an effective synthesis of the suitability of freshwater incubation and rearing environments. However, in Owikeno Lake it is extremely difficult to obtain reliable estimates of female spawner numbers, smolt numbers, and smolt size (Rutherford and Wood 2000). Appropriate limnological data provide the means to make a direct assessment of the freshwater environment, and also enable comparisons to be made between past and present conditions in Owikeno Lake. Limnological studies of varying focus, duration, and intensity were carried out on Owikeno Lake in the 1950's (Foskett 1958), 1960's (Ruggles 1965; Narver 1969), and 1970's (Chernoff 1971; Stockner and Shortreed 1979). After the 1970's no limnological studies were carried out, although some types of limnological data were occasionally collected (P. Rankin, DFO, Pacific Biological Station, Nanaimo, B.C., unpublished data; E. MacIsaac, DFO, Simon Fraser University, Burnaby, B.C., unpublished data; D. Rutherford, DFO, Pacific Biological Station, Nanaimo, B.C., unpublished data). Consequently, until the current study it was not possible to make direct comparisons of past and present physical, chemical, and biological conditions in Owikeno Lake.

This limnological investigation had three main objectives. The first was to determine the current trophic status and productivity capacity of Owikeno Lake. The second objective was to compare data collected in 2001 to data collected in the 1960's and 1970's. A third objective was to assess the potential effectiveness of lake fertilization in accelerating the recovery of Rivers Inlet sockeye salmon.

DESCRIPTION OF THE STUDY LAKE

Owikeno is a large (surface area of 94.5 km^2) lake located on British Columbia's central coast at an elevation of only 15 m. The lake is 56-km long and discharges into the head of Rivers Inlet via the 6-km long Wannock River (Fig. 1). As with much of coastal B.C., Owikeno Lake is located in the Coastal Western Hemlock biogeoclimatic zone (Farley 1979). It has cool, wet summers and mild, wet winters. Annual precipitation is heavy and is estimated to range from 250 cm to >350 cm (Farley 1979). Owikeno Lake has a large drainage basin with a total area which has been variously reported as 4,144 km^2 (Ruggles 1965) and 3,621 km^2 (Stockner and Shortreed 1979). Much of the drainage basin is further inland at substantially higher elevations (portions are heavily glaciated) and has a more continental climate than the lake itself. Most of the lake does not freeze in winter. The lake's bathymetry has not been documented using modern equipment, but Stockner and Shortreed (1979) reported the lake's mean depth as 172 m. Based on this estimate and Wannock River discharge data (Water

Survey 2001), the lake has an average water residence time of only 1.6 yr. The seasonal hydrograph is variable, but minimum flows generally occur in late winter and maximum flows in mid-summer (Water Survey 2001). This is similar to interior lakes where seasonal discharge is dominated by melting snow and ice, rather than most coastal lakes where discharge is dominated by winter rain events.

Of the lake's four basins, the two upper basins (basins 1 and 2) make up only 8% of the total lake surface area. The third basin (basin 3) is larger (20% of total area) and the lower basin (basin 4) is much larger than any of the others (72% of total surface area). Numerous tributaries of various sizes and physical characteristics enter Owikeno Lake, with the major ones entering the lake at the upper end of basin 4 (Machmell and Neechanz rivers), at the upper end of basin 3 (Sheemahant River), and in basin 1 (Inzeana Creek, Tzeo River, and Washwash River). The lake's orientation and location in steep mountainous terrain result in frequent, strong outflow winds, particularly in the lower basin.

With two notable exceptions, human influence on Owikeno Lake and its drainage basin has been minimal. First, logging, associated road building, and log handling on the lake itself have occurred since the early 1960's. Logging has occurred in the watersheds of most of the lake's larger tributaries. There is a total of 1,001 km^2 of forested area in these watersheds (total area of these watersheds is 2,414 km^2) and up to 1998, 93 km^2 had been logged (DFO 2001). Associated with this logging has been the construction of 175 km of roads. Major log handling facilities on Owikeno Lake are near the mouths of the Sheemahant and Machmell rivers.

The second major human influence on Owikeno Lake has been the commercial sockeye fishery. From 1948 to 1999, the annual catch averaged 0.52 million sockeye (range: <0.01-2.7 million) (Rutherford and Wood 2000). In the first half of the 20th century, the average catch was even higher (McKinnell et al. 2001). Based on the 1948-1999 catch, these sockeye comprised an average annual nutrient loss to the lake and its tributaries of 6.9 tonnes of phosphorus and 37 tonnes of nitrogen.

METHODS

We collected limnological data from four locations in Owikeno Lake once monthly (n=6) from May to October of 2001. We numbered the lake's basins from 1 (uppermost basin) to 4 (lowest, or main basin). Station 1 was in basin 1, station 2 was in basin 3, and stations 3 and 4 were in basin 4 (Fig. 1). Temperature and conductivity profiles from the surface to 100 m or the lake bottom (only at station 1 was the depth <100 m) were obtained at each station with an Applied Microsystems conductivity, temperature and depth meter (Model STD-12). Thermocline depths were estimated by a visual inspection of plotted temperature and depth data. Isotherms were plotted by the SAS procedure Gcontour (SAS Institute Inc. 1990) from a grid of interpolated and smoothed unscaled data computed by the SAS procedure G3grid. A Li-Cor data logger (model LI-1000) equipped with a spherical quantum sensor (model LI-193SA) was used to measure photosynthetically active radiation (400-700 nm) and determine euphotic zone depth (1% of surface intensity). A standard 22-cm white Secchi disk was used to measure water transparency.

We used an opaque Van Dorn bottle to collect all water samples. Sampling took place between 0800 and 1100 h (PST). At each station, water from 4-6 depths within the euphotic zone was collected and equal volumes mixed in 9-L Nalge Lowboy carboys to provide an integrated sample. Also at every station a hypolimnetic water sample was collected from a

depth of 50 m. Replicate analyses for turbidity, dissolved reactive silica, particulate carbon, nitrogen (particulate, ammonia, nitrate), phosphorus (total, particulate, dissolved, soluble reactive, turbidity blank) were carried out on each integrated sample. A single sample for total dissolved solids was also collected from each integrated sample. At stations 2 and 4, additional replicate samples for phytoplankton, picoplankton, and bacteria enumeration were collected. Also at stations 2 and 4, we collected discrete water samples from eight depths from the surface to 50 m. These samples were collected in 1-L polyethylene bottles and later analyzed for turbidity, nitrate, and chlorophyll. At every station dissolved oxygen concentration was determined at the water surface and at a depth of 50 m.

Chemical analyses were carried out according to methods given in Stephens and Brandstaetter (1983) and Stainton et al. (1977). For total phosphorus determination, clean screw-capped test tubes were rinsed with sample, filled, capped, stored at 4°C, and later analyzed using a molybdenum blue method after persulfate digestion. To correct total phosphorus concentrations for turbidity, a turbidity blank was run and these values were subtracted from total phosphorus (Koenings et al. 1987). Water for dissolved nutrient analyses was filtered through an ashed 47-mm diameter Micro Filtration Systems (MFS) borosilicate microfiber filter (equivalent to a Whatman GF/F filter). Each filter was placed in a 47-mm Swinnex filtering unit (Millipore Corp.), rinsed with 150 mL of distilled, deionized water (DDW), and then rinsed with approximately 50 mL of sample. For dissolved phosphorus determination, filtered water was treated as for total phosphorus, including the use of turbidity blanks. Other water samples for dissolved nutrient were kept cool and dark for 2-4 h, filtered into a clean, rinsed polyethylene bottle, and frozen. For determination of particulate phosphorus concentration, we filtered 1-L of water through an ashed 47-mm diameter MFS filter, placed the filter in a clean scintillation vial, and later analyzed it using the method of Stainton et al. (1977). For chlorophyll analysis, we filtered 250-mL of water through a 47-mm diameter, 0.45-µm Millipore HA filter. Filters were folded in half, placed in aluminum foil dishes, and frozen. They were later analyzed using a Turner fluorometer (Model 112) after maceration in 90% acetone.

Water for bacterioplankton enumeration was collected in sterile scintillation vials and preserved with two drops of formaldehyde. Bacterioplankton were later counted using the DAPI method (Robarts and Sephton 1981). Ten random fields were counted on each filter and the counts converted to numbers/mL.

For nano- and microphytoplankton enumeration and identification opaque 125-mL polyethylene bottles were rinsed with sample, filled, and fixed with 1-mL of Lugol's iodine solution. For analysis, each sample was gently mixed and a subsample was settled overnight in a 27-mL settling chamber. Transects at 187.5X and 750X magnification were counted using a Wild M40 inverted microscope equipped with phase contrast optics. Cells were identified to genus or species and assigned to size classes. Phototrophic picoplankton (cyanobacteria and eukaryotic algae <2 µm in diameter) were enumerated using the method described by MacIsaac and Stockner (1985). Within several hours of sample collection, 15 mL of sample water was filtered through a 0.2-µm Nuclepore filter counter-stained with Irgalan black. Care was taken to minimize exposure of the sample to light during sampling and laboratory processing. Filters were placed in opaque petri dishes, air-dried and stored in the dark at room temperature until analyzed. During analysis, each filter was placed on a wet 40-µm mesh nylon screen in a filter holder, 1-2 mL of filtered DDW were added to the filter column, and the cells on the filter were rehydrated for 3-5 min. Water was drawn through at a vacuum pressure of 20-cm Hg, and the moist filter was placed on a glass slide with a drop of immersion oil (Cargille Type B) and a coverslip. The Zeiss epifluorescence microscope used for picoplankton enumeration was equipped with a 397-nm longwave-pass exciter filter and a 560-nm shortwave-pass exciter filter,

a 580-nm beam-splitter mirror and a 590-nm longwave-pass barrier filter. Filters were examined at 1250X magnification under oil immersion, and 30 random fields were counted. Phototrophic picoplankton were placed in categories based on morphological characteristics, fluorescence color, and size categories (Stockner and Shortreed 1991).

We measured *in situ* photosynthetic rates (PR) at every sampling date and station. PR was determined at 7 depths from the surface to below the euphotic zone. At each depth two light and one dark glass bottles were filled, inoculated with approximately 137 kBq of a ^{14}C-bicarbonate stock solution, and incubated at the original sampling depth. To determine activity of the stock solution, at each station we inoculated three scintillation vials containing 0.5 mL of 0.2-N NaOH with the stock. Incubations lasted 1.5-2 h, usually between 1000 and 1300 h (PST).

Also at each of these depths, water for pH and alkalinity determinations was collected in 125-mL glass bottles. Within 4 hr of collection, a Cole-Parmer Digi-Sense pH meter (Model 5986-10) and Ross combination electrode were used to determine pH and total alkalinity (mg $CaCO_3$/L) according to the standard potentiometric method of APHA (1998). Dissolved inorganic carbon (DIC) concentrations were calculated indirectly from pH, temperature, total dissolved solids and bicarbonate alkalinity.

After incubation, bottles were placed in light-proof boxes and transported to the field laboratory where filtration started <2 h after incubation stopped. We filtered the entire contents of each bottle through a 25-mm diameter MFS glass fiber filter at a vacuum not exceeding 20-cm Hg. Filters were placed in scintillation vials containing 0.5 mL of 0.5-N HCl and lids were left off the vials for 6-8 hr. All vials were stored cool and in the dark. Within a few days of the incubations, 10 mL of Scintiverse II (Fisher Scientific) was added to each scintillation vial and samples were counted in a Beckman Coulter LS6500 liquid scintillation counter. Quench series composed of the same scintillation cocktail and filters used for samples were used to determine counting efficiency and the equation of Strickland and Parsons (1972) was used to calculate hourly PR. PR was converted from hourly to daily rates using methods described by Koenings et al. (1987).

Replicate zooplankton samples were collected at every station with a 160-µm mesh Wisconsin net (mouth area = 0.05 m^2) hauled vertically to the surface from 50 m. All samples were placed in 125-mL plastic bottles and preserved in a sucrose-buffered 4% formalin solution (Haney and Hall 1973). Zooplankton (all zooplankton except rotifers and nauplii, which were not counted) were later counted, identified to genus or species (Pennak 1978; Balcer et al. 1984; Dussart and Defaye (1983), and measured with a computerized video measuring system (MacLellan et al. 1993). Measurement of body length was carried out as described by Koenings et al. (1987). Zooplankton biomass (milligrams dry weight) was calculated with species-specific length-weight regressions adapted from Bird and Prairie (1985), Culver et al. (1985), Stemberger and Gilbert (1987), and Yan and Mackie (1987).

Surface area of the lake and each of its basins was determined by digitizing the lake shoreline from 1:50,000 topographic maps using Sigmascan v1.2 image analysis software. Seasonal averages of data from each station were calculated as time-weighted means of data obtained from May to October. Seasonal average PR was computed by assuming PR was zero on May 1 and October 31. Whole-lake averages were calculated by weighting the value for each station by the proportion of the lake it represented. Station 1 was weighted by the area of the 2 uppermost basins (8% of total surface area) and station 2 by the area (19.5 km^2 or 20%)

of basin 3. Stations 3 and 4, located in the large lower basin, represented 29% and 43%, of the total lake area.

RESULTS

PHYSICAL

By the first sampling date in late May of 2001, all stations exhibited some degree of thermal stratification (Fig. 2, 3). Seasonal thermoclines persisted into October, but were relatively deep throughout the growing season, with seasonal average thermocline depths ranging from 25 m in basin 1 to 45 m in basin 4 (Table 1). Highest recorded surface temperatures occurred in mid-summer and ranged from 13.9°C at station 3 to 17.2°C at station 1 (Fig. 4). At all stations, mean turbidity in the surface waters was lowest (<2 NTU) in spring. Seasonal maxima in turbidity occurred in July or August and ranged from 3.8 NTU at station 1 to 9.3 NTU at station 3 (Fig. 4). Seasonal average turbidity ranged from 2.2 NTU (station 1) to 6.3 NTU at station 3 (Table 1). Average euphotic zone depths (EZD) were deepest (7.3 m) at station 1 and shallowest (4.4 m) at station 3. At stations 2-4 the seasonal maxima in EZD of 6-8 m occurred in May or June. At these stations the EZD decreased substantially from June to July and then remained relatively constant for the remainder of the growing season (Fig. 5). There was little seasonal variation in EZD at station 1.

CHEMICAL

Seasonal average conductivity in the euphotic zone ranged from 19 µS/cm at station 1 to 26 µS/cm at station 4. In much of the lake, conductivity increased only slightly with depth, but below the thermocline in basin 1, conductivity increased rapidly to >40 µS/cm. Total dissolved solids ranged from 13-23 mg/L and total alkalinities from 5.3-10.2 mg $CaCO_3$/L, both of which are relatively low and reflect the low ionic strength of Owikeno water (Table 1). The lake was slightly acidic, with an average pH ranging from 6.37-6.63. Dissolved oxygen (DO) concentrations remained high throughout the study and averaged 11.3-11.8 mg/L at the surface. Hypolimnetic (50 m) DO was only slightly lower (9.3-11.5 mg/L).

Seasonal average EZD nitrate concentration increased from a low of 23.9 µg N/L at station 1 to 33.1 µg N/L at station 4 (Table 1). Seasonal average hypolimnetic nitrate was substantially higher and ranged from 139 µg N/L at station 1 to 49 µg N/L at station 4. EZD nitrate concentrations were highest in May, decreased to seasonal minima of <3 µg N/L at stations 1 and 2 in August, and to minima of 22 µg N/L at stations 3 and 4 in September (Fig. 6). In summer, near-surface nitrate concentrations were reduced to <25 µg N/L (approximately one-half hypolimnetic concentrations) at station 4, while at stations 1 and 2 near-surface nitrate decreased to much less (<5 µg N/L) than hypolimnetic concentrations (Fig. 6, 7).

After correction for turbidity, seasonal average total phosphorus (TP) concentration in the EZD ranged from 4.1 µg/L at station 1 to 9.4 µg/L at station 3 (Table 1). Since the first sampling date in May was after the onset of thermal stratification, the best analogue for spring overturn TP was spring hypolimnetic TP, which ranged from 3.4-5.4 µg/L (Table 1). Spring hypolimnetic total dissolved P was slightly lower, ranging from 3.0-4.5 µg/L , with a whole-lake average of 3.7 µg/L. Average EZD soluble reactive phosphorus (SRP) was substantially lower and ranged from 0.6-2.0 µg/L. At stations 3 and 4 in basin 4, SRP was lowest (<1.0 µg/L) in May and then increased to concentrations of 2.7-3.6 µg/L in October. At stations 1 and 2, less

temporal variation occurred, although highest seasonal SRP concentrations of 1.3-1.9 µg/L occurred in fall.

BIOLOGICAL

Seasonal average bacterioplankton numbers were 0.74×10^6/mL at station 2 and 0.84×10^6/mL at Station 4. At both stations seasonal maxima of $0.92\text{-}1.22 \times 10^6$/mL occurred in July.

Seasonal average photosynthetic rates (PR) were lowest (86 mg $C \cdot m^{-2} \cdot d^{-1}$) at station 4 and highest (148 mg $C \cdot m^{-2} \cdot d^{-1}$) at station 2 (Table 1). Whole-lake seasonal average PR was 113 mg $C \cdot m^{-2} \cdot d^{-1}$. There was substantial seasonal variation, with highest seasonal PR occurring in August at stations 1, 2, and 4 and in June at station 3 (Fig. 8). Vertical PR profiles were clearly indicative of the rapid light attenuation in much of Owikeno Lake. In August, highest PR occurred within 2 m of the surface and then declined rapidly to negligible levels at 5-6 m. Vertical attenuation of PR was greatest at stations 3 and 4, where euphotic zones were shallowest. Seasonal average chlorophyll concentrations ranged from 0.98 µg/L at station 4 to 1.50 µg/L at station 2 (Table 1). Chlorophyll concentrations were highest in late August at all stations except for station 1, where maximum concentration occurred in September (Fig. 8). Discrete vertical profiles of chlorophyll were collected at stations 2 and 4. On most sampling dates at station 2, concentrations in the upper 5 m of the water column were substantially higher than those in deeper water. At station 4, near-surface concentrations were also higher than deeper concentrations, but differences were not as great.

Seasonal average picoplankton numbers were 10x greater at Station 4 (1.35×10^4/mL) than at Station 2 (1.38×10^3/mL) (Table 1). At station 4, highest numbers (2.90×10^4/mL) occurred in August and the lowest (5.0×10^3/mL) in July. At station 2, no obvious seasonal trends occurred. *Synechococcus* were the most abundant picoplankton and comprised 87% of total picoplankton numbers at Station 2 and 81% of the total at Station 4. A unicellular eukaryotic picoplankton made up most of the remainder. Seasonal average nanoplankton numbers averaged 2.5×10^3/mL at station 2 and 3.2×10^3/mL at station 4. The unicellular flagellates *Chromulina* spp. and *Chroomonas* sp. were the most abundant nanoplankton. Average microplankton numbers were 6.4×10^2/mL and 9.6×10^2/mL at stations 2 and 4, respectively. The diatom *Rhizosolenia* sp. was the predominant microplankton.

Seasonal average zooplankton biomass ranged from 207 mg dry wt/m^2 at station 4 to 384 mg dry wt/m^2 at station 1 (Table 1). At stations 2-4, zooplankton biomass was lowest in May and October, with seasonal maxima occurring July or August (Fig. 9, 10). At station 1 in the uppermost basin, highest biomass occurred in May (Fig. 9). The calanoid copepod *Hesperodiaptomus* (*H. kenai* and *H. franciscanus*) dominated the zooplankton community at all stations and times (Fig. 9, 10). Its average biomass ranged from 203-355 mg dry wt/m^2 and made up from 74-98% of total zooplankton biomass. *Acanthocyclops* (primarily *A. vernalis*) was the only other common copepod. It was more abundant at station 1 (seasonal average of 24 mg dry wt/m^2) than in the remainder of the lake, where it averaged <10 mg dry wt/m^2 (Table 1).

Throughout the lake, cladoceran biomass was much less than copepod biomass. *Daphnia* was relatively abundant in spring and early summer at station 1 (seasonal average of 75 mg dry wt/m^2 and 19% of total biomass), but was rare at the other stations (Table 1). *Ceriodaphnia* was relatively abundant at station 2 in August and September (seasonal average

of 24 mg dry wt/m^2) but was rare or absent at other stations. *Bosmina* was present but rare at all stations.

DISCUSSION

TROPHIC STATUS AND LIMITING FACTORS

Assessment of total phosphorus (TP) concentration in glacially turbid lakes can be problematic. First, in the analytical procedure light backscattering caused by the turbid water results in increased absorbance peaks and artificially high P values. This can be corrected for by subtracting turbidity blanks from peak heights (Koenings et al. 1987). All TP data presented in this report have been corrected using turbidity blanks. An additional difficulty is that in glacially turbid water a substantial but variable proportion of phosphorus may be present as apatite, which can be biologically unavailable. Apatite is a common mineral found in the source rocks producing glacial debris (Reid et al. 1980). Furthermore, standard persulfate digestion procedures for TP extract some proportion of the apatite-P. In our Owikeno data, the influence of turbidity on P concentration is illustrated by the strong correlation between TP (uncorrected for turbidity) and turbidity (NTU) (r^2=0.73, n=23, $p<0.01$). Once corrected for turbidity, TP was still correlated (r^2=0.41, n=21, $p<0.01$) with turbidity, likely indicating the influence of the extraction of apatite-P on the TP data. Because Owikeno water was relatively clear in May (turbidity ranged from 0.9-1.6 NTU), spring phosphorus concentrations were likely less affected by apatite, and the spring hypolimnetic TP range of 3.4-5.4 µg/L (whole-lake average was 4.2 µg/L) places the lake in the lower to middle range of oligotrophy (Vollenweider 1976). Total dissolved phosphorus (TDP) is less affected by apatite-P, and in Owikeno Lake TDP is likely a better indicator of concentrations of biologically available P. While slightly lower than TP, the whole-lake average TDP of 3.7 µg/L placed the lake in a similar trophic range as TP. Both the TP and TDP data are higher than those found in many other lakes on B.C.'s coast (Shortreed et al. 2001). Nitrate concentrations were also higher than usually observed in coastal sockeye nursery lakes (Shortreed et al. 2001). Phosphorus and nitrate data both suggest that ambient nutrient loading to Owikeno Lake is higher than in most coastal B.C. lakes.

Other limnological variables used as indicators of trophic status place Owikeno Lake in a similar trophic range. For example, Forsberg and Ryding (1980) proposed a chlorophyll-based trophic classification where oligotrophic lakes were defined as those with seasonal average chlorophyll concentrations of <3 µg/L. Owikeno Lake's average chlorophyll concentration of 0.98-1.50 µg/L was in this oligotrophic range. Bird and Kalff (1984) proposed a trophic classification where oligotrophic lakes had bacteria numbers <1.7 x 10^6/mL. Average bacteria numbers in Owikeno Lake were 0.74x10^6/mL and 0.84x10^6/mL at stations 2 and 4, respectively. The seasonal average photosynthetic rate of 113 mg $C \cdot m^{-2} \cdot d^{-1}$ was lower than the average of 147 mg $C \cdot m^{-2} \cdot d^{-1}$ reported for a number of Fraser system sockeye lakes, but was higher than the average of 89 mg $C \cdot m^{-2} \cdot d^{-1}$ reported for coastal sockeye lakes (Shortreed et al. 2001). Moreover, given that the average euphotic zone depth (8.5 m) for these other coastal lakes was 1.6x deeper than Owikeno Lake's average of 5.1 m, average volumetric photosynthetic rates were substantially higher in Owikeno than in most other coastal lakes. The productivity to biomass ratio (P/B) (µg $C \cdot$µg $Chl \cdot d^{-1}$), commonly called the assimilation ratio, is a useful indicator of the turnover rate of the phytoplankton community. The average P/B ratio in Owikeno Lake was 16, substantially higher than the average of 11 found in the other coastal lakes (Shortreed et al. 2001). These data clearly indicate that while Owikeno Lake is oligotrophic, it is more productive than many other sockeye nursery lakes in coastal B.C.

Ratios of sestonic carbon, nitrogen, phosphorus, and chlorophyll (C:N, C:P, N:P, C:Chl) have often been used as indicators of phytoplankton nutrient deficiency (Healey and Hendzel 1980; Hecky et al. 1993). The degree of P limitation increases with increasing C:P and N:P ratios and the degree of N limitation with increasing C:N ratios. Seasonal averages of these variables are normally used in these calculations. However, in Owikeno Lake, summer and fall particulate P values were erroneously high because of the contribution of apatite-P. In May, however, turbidities at all stations were <2 NTU. Consequently, only data collected in May were suitable for these calculations (Table 1). Because May is near the start of the growing season, nutrient deficiencies would be less pronounced than those in summer or early fall. Nevertheless, they do provide some insight into conditions in Owikeno Lake. At stations 2 and 3, C:N:P ratios were lower than at stations 1 and 4 (indicating less P deficiency), possibly because of the proximity of these stations to nutrient input from the Sheemahant and Machmell rivers (Table 1). To place Owikeno Lake in perspective, we compared spring C:N:P ratios in Owikeno Lake with spring ratios in 13 sockeye nursery lakes of varying trophic status in the Fraser and Skeena river systems (Nidle and Shortreed 1996; Shortreed et al. 1998, 2000; K. Shortreed, unpublished data). Owikeno Lake's whole-lake average spring C:N:P ratio of 164:16:1 was substantially lower than the average of 262:22:1 for these 13 lakes, and in only 3 of the 13 lakes were N:P ratios lower than in Owikeno Lake. These data indicate that, in spring, P limitation in Owikeno Lake is not as strong as it is in many other B.C. sockeye lakes.

SPATIAL/TEMPORAL HETEROGENEITY

Owikeno Lake exhibited considerable spatial heterogeneity in a number of variables as a result of its multiple basins and the large number of tributaries. The uppermost basin (basin 1) was the clearest, had the most stable and shallowest thermal structure, and its surface waters had the lowest ionic strength. Major tributaries entering basin 1 were relatively clear (Rutherford et al. 1998). Hypolimnetic nitrate concentrations were higher in basin 1 than in the remainder of the lake and soluble reactive phosphorus concentrations were lower. These data suggest that tributaries entering basin 1 had higher nitrogen concentrations than other lake tributaries. Soluble reactive phosphorus concentrations at stations 2-4 suggest that the large tributaries entering the upper ends of basins 3 and 4 (the Sheemahant and Machmell rivers) had higher phosphorus concentrations than those entering basin 1. These differences in nutrient loading likely resulted in observed differences in some biological variables. Seasonal average chlorophyll and PR were higher at stations 2 and 3, which were closest to the influence of the Sheemahant and the Machmell rivers. Despite the relatively high turbidity of the Sheemahant and the Machmell rivers, it appears they stimulate lake productivity.

With some exceptions, Owikeno Lake's zooplankton community exhibited less spatial heterogeneity than other variables. Biomass was higher in basin 1 and in the upper portion of basin 4 than elsewhere in the lake. Zooplankton species composition was unusually simple, with only one genus (*Hesperodiaptomus*) comprising an average of 74-98% of total biomass. Of the cladocerans, *Daphnia* was relatively abundant (19% of total biomass) only at station 1 and *Ceriodaphnia* (10% of total biomass) was relatively abundant only at station 2. On a whole-lake basis, cladocerans comprised only 4% of total biomass. This low abundance has been observed in a number of similar (oligotrophic, cold, glacially turbid) Alaskan lakes and attributed to excessive energetic costs in cladoceran filtering and feeding rates (Koenings et al. 1990). In conjunction with low temperatures and food levels, turbidities as low as 5-10 NTU can exclude cladocerans from a lake's plankton community (Koenings et al. 1990). While Owikeno Lake is relatively clear in spring, turbidities in basin 4 were 7-9 NTU for much of the growing season. These data suggest that regardless of planktivore density, much of the lake is physically unsuitable for cladocerans.

In 2001, Owikeno Lake's average zooplankton biomass of 276 mg dry wt/m² was substantially less than that found in most sockeye nursery lakes in the B.C. interior, but was higher than that found in many coastal sockeye nursery lakes (Shortreed et al. 2001), providing further evidence that it is more productive than most of these coastal lakes. However, in 2001 sockeye fry density and subsequent grazing pressure on the zooplankton community was among the lowest ever recorded in Owikeno Lake. It is likely that zooplankton biomass was lower when grazing pressure was higher.

PRODUCTIVE CAPACITY

Rearing capacity of a sockeye nursery lake has been estimated in several ways. Hume et al. (1996) utilized fry models (spawner numbers to fall fry or smolt numbers) to estimate rearing capacity. Hume et al. (1996) and Shortreed et al. (2000) developed the PR model, a modification of an Alaskan rearing capacity model (Koenings and Kyle 1997). This model utilizes photosynthetic rates to predict maximum potential smolt production. In Owikeno Lake, available data on spawners and juveniles are not adequate to utilize fry models similar to those presented by Hume et al. (1996). However, photosynthetic rate (PR) data are available, so with some revisions the PR model can be used to make predictions of the sockeye rearing capacity of Owikeno Lake.

Based on a seasonal average PR of 113 mg $C \cdot m^{-2} \cdot d^{-1}$, the PR model predicts a maximum smolt production from Owikeno Lake of 87 tonnes (Shortreed et al. 2000). To convert from biomass to number of smolts, the PR model uses an average smolt weight of 4.5 g. However, Owikeno smolts are substantially smaller than this. In 26 years between the late 1950's and the late 1990's, Owikeno sockeye presmolts averaged 1.42 g (Rutherford et al. 1998; McKinnell et al. 2001). These presmolts were collected using either a 1-m diameter conical trawl (1950's and 1960's) (Ruggles 1965; Chernoff 1971) or a 2x2-m beam trawl (1980's and 1990's). Trawls of this size are increasingly size-selective after fish length exceeds 40 mm (K. Hyatt, DFO, Pacific Biological Station, Nanaimo, B.C., personal communication). However, this size-selectivity is predictable and smolt lengths and weights can be calculated from trawl-caught presmolts. Once this correction was applied (Smolt wt = 2.25 x Trawl wt - 0.88, $r^2=0.71$, $p<0.01$) (P. Rankin, DFO, Pacific Biological Station, Nanaimo, B.C., personal communication), overall average smolt weight in Owikeno Lake increased to 2.33 g (range: 1.0-5.5 g). Using this average weight and the predicted maximum biomass, the PR model predicts a maximum production of 37 million smolts. Implicit in predictions from the PR model is that all sockeye migrate as age-1 smolts and that no competitors are present. Presence of limnetic species which can compete with age-0 sockeye such as three-spine stickleback (*Gasterosteus aculeatus*), kokanee, age-1 sockeye, and mysids will reduce a lake's sockeye rearing capacity. The proportion of age-1 sockeye fry is extremely low in Owikeno Lake (Rutherford and Wood 2000), but the three-spine stickleback is occasionally relatively abundant in the lake's limnetic zone (Ruggles 1965; Chernoff 1971). Although its actual density is unknown, for several years in the early 1960's, Ruggles (1965) reported that it comprised 12% of total captured limnetic fish. In these years, sockeye escapements averaged 0.59 million, so it is probable that these were years when the lake's rearing capacity was nearing full utilization. Consequently, we reduced the PR model prediction by 12% to account for these other limnetic planktivores, which resulted in a predicted maximum smolt output of 33 million. If Owikeno Lake produced 4.5 g smolts, the PR model predicts it would require an escapement of 0.3 million to produce maximum smolt biomass. Since Owikeno smolts average only 2.33 g, it would require more smolts to produce maximum biomass and consequently more adult spawners. The revised prediction is that 0.6 million spawners would be required to produce maximum smolt biomass.

Historically, estimated escapements of >0.5 million occurred in 12 of the 52 years from 1948 to 2000.

A number of studies have reported that sockeye smolt-to-adult survival decreases with decreasing smolt size (Ricker 1962; Hyatt and Stockner 1985; Koenings and Burkett 1987; Koenings et al. 1993; Bradford et al. 2000). Koenings et al. (1993) reported an average smolt-to-adult survival of 3% for smolts 60-65 mm in length from lakes located at latitudes <55°N. Although Owikeno smolts from high density brood years are smaller yet, if 3% is used as an average smolt-to-adult survival rate, the PR model predicts an adult return of one million sockeye. Available total return data to Owikeno Lake are potentially unreliable because of uncertainties in escapement estimates (McKinnell et al. 2001), but available estimates are that total returns to Owikeno Lake averaged 0.9 million (range: <0.01-3.6 million) in the years 1948-1999 (Rutherford et al. 2000).

NUTRIENT LOADING (CARCASSES AND THE FISHERY)

While the importance of sockeye carcasses and their marine-derived nutrients (MDN) to freshwater productivity has been recognized for decades (Ricker 1937), only in recent years has this received substantial attention (Larkin and Slaney 1997; Schmidt et al. 1998). Mathisen et al. (1988) reported that a pre-spawning adult sockeye weighed an average of 2.7 kg and contained 0.485% P and 2.67% N. Assuming values for Owikeno sockeye are similar, each adult spawner brings 13 g of marine-derived P and 72 g of marine-derived N back to freshwater. As previously mentioned, escapement data to Owikeno Lake are somewhat uncertain, but they do enable at least a first estimate of the importance of sockeye spawners and their marine-derived nutrients to the lake's productivity. In the years 1948-1999, estimated average escapement to Owikeno Lake was 0.38 million (range:<0.01-1.50 million). In the same period, numbers of sockeye removed each year by the commercial fishery averaged 0.52 million (range:<0.01-2.7 million) (Rutherford and Wood 2000). Based on these estimates, in the years 1948-1999 sockeye spawners provided from <0.05-20 t P (average = 5.0 t P). In the same period, sockeye annually removed by the fishery contained from <0.01-36 t P (average = 6.9 t P). Other less abundant salmon species such as chinook (*O. tshawytscha*) and coho (*O. kisutch*) originated from streams in the Owikeno watershed and were harvested by various fisheries, resulting in further reductions in the input of MDN. The actual amount of MDN delivered to the lake would be somewhat lower than these figures indicate because of ecosystem processes in the lake's spawning streams. Many species of insects, fish, birds, and mammals feed directly on salmon carcasses and riparian vegetation also retains MDN (Cederholm et al. 1989; Bilby et al. 1998).

It would be useful to determine if salmon carcasses were a substantial source of nutrients to Owikeno Lake or if its high flushing rate made the contribution of MDN insignificant. A number of empirical phosphorus loading models have been developed for North American lakes (Reckhow and Chapra 1983). Predicted phosphorus loads from these models differ because of differences in the suite of lakes used in development of each model. Further, Owikeno Lake is larger and deeper than most lakes used in development of these models, so their predictions for Owikeno Lake must be viewed with caution. A further caveat is that the models do not differentiate between biologically available and unavailable (apatite) P. Because the P load to Owikeno Lake contains apatite-P, model predictions will overestimate the actual P load to the lake. Despite these limitations, the models do provide a first approximation of the lake's P load and the importance of MDN to this load. Two of the most widely used models are those of Vollenweider (1976) and Reckhow (1979).

The Vollenweider model predicts the annual P (L_p) load to a lake with the following equation:

$$L_p \text{ (mg P·m}^{-2}\text{·yr}^{-1}\text{)} = \frac{TP_{spr} \times \bar{z}\left(1+\sqrt{T_w}\right)}{T_w}$$

The Reckhow model takes the following form:

$$L_p \text{ (mg P·m}^{-2}\text{·yr}^{-1}\text{)} = TP_{spr} \times (11.6 + 1.2 \times \frac{\bar{z}}{T_w})$$

where: TP_{spr} =spring overturn total P (µg/L)

T_w = water residence time (yr)

$\bar{z}$ = mean depth (m)

Using the May 2001 hypolimnetic TDP concentration of 3.7 µg/L as a surrogate for spring overturn TP, a mean depth of 172 m, and a water residence time of 1.6 yr, the Vollenweider model results in an L_p of 901 mg P·m^{-2}·yr^{-1}, or a total annual P load of 85 tonnes. The Reckhow model yields a somewhat lower result of 520 mg P·m^{-2}·yr^{-1} (49 tonnes P). Given that sockeye escapements in the two years previous to 2001 were among the lowest on record, it can be assumed that carcass contribution to the 2001 P load was minimal.

Using the Vollenweider model and the available catch and escapement data, in the years 1948-1999 sockeye spawners made an average contribution of 5% (range: <0.1-19%) of the lake's total P load. In the same period, sockeye removed by the fishery represented an average annual reduction in the lake's P load of 6% (range:<0.01-27%). From the Reckhow model, in the same period sockeye spawners made an average contribution of 9% (range: <0.1-29%) of the lake's total P load. Sockeye removed by the fishery in those years represented an average reduction in the P load of 10% (range:<0.1-37%). It should be emphasized that if corrections could be applied to account for the proportion of apatite-P, the relative carcass contribution to the total P load would increase.

To place the carcass P load in perspective, lake fertilization programs on lakes of Owikeno's size have added 6-8 tonnes P and have resulted in substantial increases in productivity (Stockner and MacIsaac 1996). No doubt, nutrients from a fertilization program which are added directly to a lake's euphotic zone during the growing season are more efficiently utilized by phytoplankton than MDN. While the importance of MDN to Owikeno Lake productivity cannot be more than roughly estimated with available data and models, its impact cannot be dismissed as insignificant, nor can it be concluded that a century of lost MDN through the commercial harvest has not reduced the lake's productive capacity. An interesting observation appeared in Foskett (1958), who reported on data collected in Owikeno Lake from 1951-1954. He stated that phytoplankton blooms of sufficient magnitude to plug plankton nets and to show up as "rows of green" along the shore occurred in fall in the lake's upper basins. He attributed these blooms to an influx of nutrients from sockeye carcasses. These blooms were not observed in 1978 or 2001, when escapements were only 30% and 3%, respectively, of the 0.63 million average escapement from 1951-1954. Given the small size of the upper basin, and the large number of spawners its tributaries could accommodate, it is possible that the effect of carcass nutrients was most pronounced in that area of the lake.

COMPARISON WITH PREVIOUS STUDIES

Comparisons with previous studies would help determine whether Owikeno Lake's rearing environment has changed in the last 40 years. Limnological data collected in a number of previous investigations (Foskett 1958; Ruggles 1965; Chernoff 1971; Stockner and Shortreed 1979; P. Rankin, DFO, Pacific Biological Station, Nanaimo, B.C., unpublished data; D. Rutherford, DFO, Pacific Biological Station, Nanaimo, B.C., unpublished data) allow some comparisons to be made between limnological conditions in 2001 and those in the 1950's, 1960's, 1970's, and 1980's.

Seasonal surface temperature data are available from 1960-1963, 1978, and 2001. Because of differing station locations in some of the studies, valid comparisons could only be made between the upper basin (basin 1) and the "lower" basin (combined basins 3 and 4). Although there is substantial annual variation, surface temperature data from 1978 and 2001 are within the range recorded from 1960-1963 (Fig. 11). In basin 1, seasonal surface temperatures averaged 11.5°C (range: 10.5-12.9°C) in the 1960's, 12.5°C in 1978, and 12.1°C in 2001. From 1960-1963, seasonal average surface temperatures in the "lower" basin ranged from 10.9-12.4°C (average = 11.9°C), while averages were 11.7°C in both 1978 and 2001.

In 1978, light data used to calculate euphotic zone depths were collected using a Li-Cor Model LI-192S quantum sensor (Stockner and Shortreed 1979). In 2001, we used a Li-Cor spherical quantum sensor (model LI-193SA). Although both sensors measure photosynthetically active radiation (400-700 nm), their different configurations yield slightly different results. However, euphotic zone depths computed from data collected with the two sensors are highly correlated ($EZD_{spherical}=1.1075xEZD_{quantum}$, $r^2=0.96$) (K. Shortreed, data on file), so the earlier data were adjusted by this factor prior to making comparisons. Spatial and temporal variation in EZD followed similar patterns in both 1978 and 2001, with the clearest water and the least seasonal variation occurring at station 1 (Fig. 12). In both years at stations 2 and 4, clearest water occurred in spring, followed by declines to near seasonal minima in summer, with relatively little change for the remainder of the sampling period. Seasonal average EZD were similar in both years, ranging from 4.5-6.9 m in 1978 and from 4.9-7.3 m in 2001. Whole-lake average EZD was 5.1 m in both years.

Substantially more data on Secchi depth than EZD are available, with seasonal data available from the early 1960's (Ruggles 1965), 1978 (Stockner and Shortreed 1979), 1988 (P. Rankin, DFO, Pacific Biological Station, Nanaimo, B.C., unpublished data), and 2001 (this study). Because of differing station locations in the various studies, valid comparisons could only be made between the upper basin (basin 1) and the "lower "basin (combined basins 3 and 4). Although substantial annual variability in Secchi depth is apparent, spatial and temporal variation in 2001 was generally similar to that in the preceding four decades (Fig. 13). Seasonal averages were also similar. In the "lower" basin, seasonal average Secchi depth ranged from 1.3 m in the 1960's to 1.7 m in 2001. In the upper basin, it ranged from 2.5 m in the 1960's to 2.8 m in 2001. In both 1978 and 1988 average Secchi depths were 1.6 m in the lower basin and 2.7 m in the upper basin.

Nitrate concentrations exhibited very similar trends in both 1978 and 2001 (Fig. 14). Average summer (June-September) euphotic zone concentrations at stations 1, 2, and 4 ranged from 16-24 µg N/L in 1978 and from 14-31 µg N/L in 2001. In both 1978 and 2001, seasonal minimum nitrate concentrations were <5 µg N/L at stations 1 and 2, and 20-25 µg N/L at station 4.

Comparable chlorophyll data are available from 1978 (Stockner and Shortreed 1979) and from 2001 (this study). In 1978, seasonal averages at stations 2 and 4 were 1.20 and 0.94 µg/L, respectively (Fig. 15). In 2001, chlorophyll exhibited more temporal variation, and seasonal averages at both stations 2 and 4 (1.50 and 0.98 µg/L, respectively) tended to be slightly higher than those in 1978. In the upper basin, seasonal average chlorophyll was substantially higher (2.02 µg/L) in 1978 and than the average of 1.01 µg/L in 2001. The reason for this difference is not known, but it could have been due to lower juvenile sockeye grazing pressure and/or to lower nutrient loading in 2001. Escapements to Owikeno Lake were approximately 188,000 in 1977 and 21,000 in 2000. This 9-fold difference no doubt resulted in higher grazing pressure on the zooplankton community in 1978. In turn, this would have resulted in lower zooplankton numbers, lower grazing pressure on the phytoplankton community, and higher phytoplankton biomass. This effect of planktivore density on phytoplankton biomass has been documented in other sockeye nursery lakes (Schmidt et al. 1998). The much higher escapement in 1977 would also have provided higher nutrient loading than in our study, which could also have contributed to higher phytoplankton biomass.

Comparable photosynthetic rate data are available from the lake only in 1978 and 2001. Limited data were reported by Narver (1969), but methodological differences preclude making comparisons. In the 1978 study, photosynthetic rate measurements were done using scintillation cocktails that were not alkalized (Stockner and Shortreed 1979). This caused systematic underestimates in the activity of the ^{14}C inocula, resulting in an overestimate of photosynthetic rates by a factor of 1.14 (Kobayashi 1978). To make comparisons with data from the current study, we divided PR data collected in 1978 by this factor. Seasonally, PR in both study years was variable, with highest values occurring in August in 2001 and in July or September in 1978 (Fig. 16). Seasonal average PR ranged from 66 to 149 mg $C \cdot m^{-2} \cdot d^{-1}$ in 1978 and from 86 to 148 mg $C \cdot m^{-2} \cdot d^{-1}$ in 2001. At station 1, average PR was higher (148) in 1978 than in 2001 (109 mg $C \cdot m^{-2} \cdot d^{-1}$), while at stations 2 and 4 PR was somewhat higher in 2001. Whole-lake seasonal average PR was 88 mg $C \cdot m^{-2} \cdot d^{-1}$ in 1978 and 113 mg $C \cdot m^{-2} \cdot d^{-1}$ in 2001, within the range of annual estimates commonly seen in B.C. lakes (Hume et al. 1996). This range in annual PR estimates may due to climatic variability (e.g. annual differences in discharge, nutrient loading, precipitation, wind, and cloud cover). Also, these estimates were obtained by sampling at relatively infrequent monthly intervals, so some short-term peaks in PR may have been missed.

Zooplankton data have been collected from Owikeno Lake on a number of occasions since the early 1950's (Foskett 1958; Ruggles 1965; Chernoff 1971; Rankin et al. 1984; P. Rankin, DFO, Pacific Biological Station, Nanaimo, B.C., unpublished data; D. Rutherford, DFO, Pacific Biological Station, Nanaimo, B.C., unpublished data). Given differences in sampling frequencies, locations, and collection methods over the 50 yr these studies span, quantitative comparisons can only be made with zooplankton data collected from the 1970's to the present. In 1978, macrozooplankton density was 2.5-3.6 times lower than in 2001 (Rankin et al. 1984) (Fig. 17). Seasonal average zooplankton numbers at stations 1, 2, and 4 ranged from 17,000-23,000/m^2 in 1978 and from 61,000-84,000/m^2 in 2001. Although abundances were quite different, community structure was similar, with *Hesperodiaptomus* and *Acanthocyclops* being the most abundant genera in both years. In the earlier study these abundant genera were called *Diaptomus* and *Cyclops*, respectively. Names of these taxa were changed to *Hesperodiaptomus* and *Acanthocyclops* in the 1980's (Dussart Defaye 1983; Balcer et al. 1984). *Daphnia* was found at station 1 in both years but was absent or very rare at stations 2 and 4. At station 1 in 1978, *Daphnia* was present in greater than trace amounts only in April, while in 2001, measurable quantities were present from May-October. The seasonal average abundance of *Daphnia* at station 1 was 7 times less in 1978 (565/m^2) than in 2001

(3,860/m^2). These differences between years can be attributed to grazing pressure, since sockeye escapements were 9-fold higher (192,000) in 1977 (Rutherford and Wood 2000) than the approximately 21,000 spawners in 2000 (Holtby 2002). Zooplankton data are also available from July and September 1992 (P. Rankin, DFO, Pacific Biological Station, Nanaimo, B.C., unpublished data) and September and October 1998 (D. Rutherford, DFO, Pacific Biological Station, Nanaimo, B.C., unpublished data). Low *Daphnia* abundance in those years relative to 2001 at equivalent times of the year can also be attributed to grazing pressure, because sockeye escapements were substantially higher in 1991 (346,000) and 1997 (275,000) (Rutherford and Wood 2000) than in 2000. Throughout the lake, the dominant zooplankton genus (*Hesperodiaptomus*) was present in greater numbers in 2001 than in earlier years (Fig. 18). The small cladoceran *Ceriodaphnia* was not reported in the lake prior to 1998 but was found in measurable quantities at stations 2 and 3 in 1998 and 2001. The reason for this is unknown but it may due lower grazing pressure in the latter part of the 1990's. In 1978, *Bosmina* was abundant at station 1 and less so at station 2 (Rankin et al. 1984), but was rare in our study. Higher grazing pressure in 1978 reduced *Daphnia* numbers and may have resulted in greater numbers of the more predation-resistant *Bosmina* (Koenings and Kyle 1997).

Although quantitative comparisons cannot be made with studies carried out prior to 1978, information from the earlier studies do provide some insight into differences between current and past zooplankton community structure. Foskett (1958) provided little zooplankton data, but did comment that *Daphnia* was the most common cladoceran and that *Cyclops* was the most common copepod. In the years of this study (1951-1954), fry present in the lake were from escapements which averaged 0.73 million, substantially higher than in any later years where zooplankton data are available. *Cyclops* are less susceptible to predation than *Hesperodiaptomus* (Koenings and Kyle 1997) and the higher grazing pressure in the 1950's may have resulted in a shift to this genus. In all later studies, *Hesperodiaptomus* was the most abundant copepod. Unfortunately, Foskett (1958) did not report on the actual abundance or location of *Daphnia* in Owikeno Lake. It has been well-documented that *Daphnia* is a preferred prey item of juvenile sockeye and if available, fry will graze on it almost exclusively (Goodlad et al. 1974; Hume et al. 1996). It is unclear why such a preferred prey item would have been the most abundant cladoceran when grazing pressure was the highest recorded.

Ruggles (1965) carried out a 4-yr (1960-1963) study of Owikeno Lake. He reported that *Daphnia* was abundant only in the upper basin, that *Hesperodiaptomus* was the most abundant genera throughout the lake, and that *Acanthocyclops* was second in abundance to *Hesperodiaptomus*. These observations agree with those in 1970 (Chernoff 1971), 1978 (Rankin et al. 1984), and with this study. Seasonal succession was also similar in all studies, with highest biomass occurring in spring in the upper basin and in summer in the lower basins.

Data on the diet of juvenile sockeye in Owikeno Lake is available only from the late summer of 1970 (Chernoff 1971). Not surprisingly, stomach contents consisted primarily of *Daphnia* where it was available (upper basin) and *Hesperodiaptomus* in the rest of the lake.

FERTILIZATION ASSESSMENT

For over 20 years, lake fertilization has been a widely used technique for increasing numbers of sockeye salmon in British Columbia and Alaska (Stockner and MacIsaac 1996; Shortreed et al. 2001). Whole-lake nutrient additions have increased productivity in lakes with a wide variety of physical and chemical environments, but there are some common prerequisites before fertilization can be successful. Obviously, for nutrient additions to stimulate production rates, ambient nutrient loading must be an important factor in maintaining low productivity. This

may not be the case in lakes with high nutrient loading, unstable water columns, or high turbidity. A stable epilimnion where temperatures are within the preferred range for sockeye is a desirable feature because added nutrients will be more effectively contained within the euphotic zone. A zooplankton community containing preferred prey items (i.e. *Daphnia*) is also desirable.

Juvenile sockeye growth rates must be low enough that a growth increment will result in improved marine survival. In general, once smolt weight averages 6-8 g, further increases in size yield relatively little improvement in marine survival (Koenings et al. 1993). Consequently, lakes with smolt weights >6 g are not generally viewed as viable candidates for fertilization.

Basins 3 and 4 of Owikeno Lake do not meet some of the usual criteria used to characterize a lake as a favorable candidate for fertilizer additions. Along with deep, relatively unstable epilimnia, these areas of the lake have relatively turbid water for much of the growing season (average euphotic zone depths range from 4.4-5.6 m). Nutrient loading appears to be somewhat higher than in many other coastal B.C. lakes. The zooplankton community is dominated by the copepod *Hesperodiaptomus*, which for sockeye is a less effective food resource than cladocerans such as *Daphnia*. Because copepods such as *Hesperodiaptomus* have longer generation times than cladocerans, accrued benefits from fertilization are likely to be less, or at least will take longer to manifest themselves in increased zooplankton numbers. In some lakes, fertilization has increased the relative abundance of cladocerans such as *Daphnia* (Hume et al. 1996), but this is unlikely to happen in basin 4 of Owikeno Lake because of constraints imposed by the lake's physical environment. For these and other reasons, lakes with characteristics like Owikeno have seldom been fertilized. However, it is worth examining results of fertilization programs on those few lakes having characteristics similar to Owikeno.

Kitlope Lake is located on Gardner Canal on B.C.'s north coast. With a surface area of only 11.9 km², it is much smaller than Owikeno, but it has some similar conditions. It is deep, fast-flushing, cold, and thermally unstable (Stockner et al. 1993). It is glacially turbid, but its average euphotic zone depth of 7.5 m is greater than Owikeno Lake's average of 5.1 m. Nutrient concentrations and photosynthetic rates are lower than in Owikeno, but zooplankton biomass is similar. Despite these conditions, the lake was fertilized in 1979 and 1980 (the lake was sampled from 1978-1980). During fertilized years, average chlorophyll concentration were 60% higher and average zooplankton biomass was 250% higher than in the unfertilized year. Sockeye smolt weights increased 2.5-fold from 2.1 g to an average of 5.2 g during the fertilized years (fish densities were similar in all years) (Hyatt and Stockner 1985). In summary, fertilization of this lake with its generally unfavorable characteristics appears to have been of benefit to its sockeye stock.

A second "case study" is Alaska's Coghill Lake (Edmundson et al. 1997). It is also much smaller (surface area=12.7 km²) than Owikeno Lake and is meromictic, with a monimolimnion starting at approximately 30 m. However, it is cold and has weak thermal stratification in the 30-m deep mixolimnion. The lake is glacially influenced with an average turbidity of 5 NTU, very similar to Owikeno Lake's average of 5.5 NTU. However, its average euphotic zone depth of 8.8 m was substantially deeper than that in basins 3 and 4 of Owikeno Lake. Phosphorus loading appeared to be similar and nitrogen loading was slightly lower. As with Owikeno Lake, its zooplankton community was dominated by copepods and it produced very small (1.5 g) smolts. During fertilization of Coghill Lake, phytoplankton biomass increased by 220% and zooplankton biomass by 117%. However, it should be noted that it took several years of fertilization before the lake's dominant copepod responded positively. Average smolt size did not increase during fertilization, but smolt production increased substantially, with increases in both total number of smolts and in smolts-per-spawner (Edmundson et al. 1997).

Results from the fertilization of Kitlope and Coghill lakes suggest that criteria often used to assess lakes as candidates for fertilization may be too conservative. In other words, lakes with physical characteristics viewed as unfavorable have responded positively to fertilization. It is not possible to categorically state whether fertilization would benefit Owikeno Lake sockeye, given current low escapements and variable marine survival rates. Conditions in basin 4 of Owikeno Lake are less favorable than those in Kitlope and Coghill lakes, but in basins 1-3 conditions are more favorable (more cladocerans and/or clearer water). Given Owikeno Lake's deep epilimnion and large surface area, substantial amounts of fertilizer would be required if the whole lake was to be fertilized. A detailed cost estimate of an Owikeno Lake fertilization program has not been done, but a rough preliminary estimate is that the annual cost would be $150,000-$200,000 (D. MacKinlay, DFO regional headquarters, Vancouver, personal communication). Also, to increase chances of success, a fertilization program would have to be carried out for many years. A somewhat less expensive alternative would be to fertilize only basins 1-3. These basins make up only 28% of total lake surface area, and whether fertilization of only these basins would be merited would depend to a large extent on the proportion of sockeye fry which rear in these areas.

Size of a lake's sockeye smolts is an important factor in assessing its suitability for fertilization. Smolt-to-adult survival increases in a curvilinear fashion with increasing smolt length (Ricker 1962; Hyatt and Stockner 1985; Koenings et al. 1993). Beyond a length of 90-100 mm, only minimal increases in marine survival occur (Koenings et al. 1993). Owikeno Lake sockeye fry exhibit strong density-dependent growth (McKinnell et al. 2001), but even at the recent low escapement levels, smolts are relatively small. Escapement in 2000 was approximately 21,000 (Holtby 2002). From April-June of 2002, a rotary screw trap in the Wannock River captured a total of 63 sockeye smolts from this brood year. These smolts averaged 80 mm in length and 4.3 g in weight (S. MacLaurin, DFO, Bella Coola, B.C., unpublished data). Even at current low escapements, Owikeno smolts are small enough that an increase in size would likely result in increased marine survival.

An important component of any restoration initiative, particularly one that requires substantial resources, is an assessment program that can detect benefits from the initiative. When effective, lake fertilization either results in bigger smolts (Hyatt and Stockner 1985) or more smolts of the same size (Lebrasseur et al. 1978). In some lakes, it produces both more and bigger smolts (Kyle 1994). Given adequate marine survival, more and/or bigger smolts usually results in more returning adults. In a lake fertilization project, changes in phyto- and zooplankton biomass or productivity are usually detectable (Stockner and Shortreed 1985). If fertilizer additions increased the productivity of Owikeno Lake, it is likely that changes in these lower trophic levels could be detected. To detect increases in smolt size as a result of fertilization, comparisons would have to be made between unfertilized and fertilized years with similar fish densities. Numbers of female spawners or acoustically-derived fry population estimates are the most reliable indicators of potential or actual fry density (Hume et al. 1996). Neither of these estimates are available for Owikeno Lake. However, there is a relatively strong relationship between summer trawl catch-per-unit-effort vs. presmolt weight (McKinnell et al. 2001). To detect increases in smolt weight during fertilization, these data would have to be outliers in this relationship. However, measured increases in presmolt weight would tend to be reduced by size biases associated with the use of a small trawl. This bias would need to be addressed before valid comparisons could be made. To detect increased in-lake survival (i.e. more smolts/spawner) during fertilization is more difficult. Ideally, reliable estimates of the numbers of females that spawned and subsequent smolt numbers need to be available. Neither

of these estimates are available for Owikeno Lake, and unfortunately increased freshwater survival would most likely be undetectable.

SUMMARY

This study examined current limnological conditions in Owikeno Lake and based on comparisons with earlier data, found no evidence that conditions in the main portion of the lake (basin 4) are less favorable for juvenile sockeye than they have been for the past several decades. Although available data are insufficient to determine whether a long-term decline in lake productivity has occurred because of a century of commercial fishing and reduced MDN, phosphorus loading models suggest this may be the case. Observations from several years in the 1950's, when escapements were high (Foskett 1958), suggest that productivity of the upper lake basins was higher in those years. Although the productive capacity of Owikeno Lake may have declined in the last 50-100 years, this does not explain the rapid decline in stock size in the 1990's. Using juvenile abundance and growth indices, McKinnell et al. (2001) concluded that poor marine survival, rather than changes in freshwater conditions, were the most likely explanation for the rapid decline in Owikeno Lake sockeye. This study provides evidence in support of the conclusion that freshwater conditions were not responsible for the decline.

Owikeno Lake is oligotrophic, but has higher nutrient loading and higher productivity than many other coastal B.C. lakes. An adjusted PR model prediction is that the lake currently has the capacity to produce 33 million smolts with an escapement of 0.6 million. Even at very low escapement levels, marine survival of Owikeno smolts would likely increase with increases in size. Fertilization of Owikeno Lake would possibly result in production increases which would benefit sockeye, but the probability of this occurring or of detecting those benefits is lower than in many other sockeye nursery lakes.

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Table 1. Seasonal (May-October) averages from 2001 except where otherwise stated,. Most presented data are integrated values from the euphotic zone. Data called hypolimnetic were collected from a depth of 50 m. On several occasions in late summer and fall at stations 3 and 4, this depth was within the metalimnion.

Variable	Station				Whole-lake average
	1	2	3	4	
Surface temperature (°C)	12.8	12.3	12.1	12.1	12.2
Mean epilimnetic temperature (°C)	10.5	11.1	11.7	11.6	11.4
Thermocline depth (m)	25	35	45	45	41
Secchi depth (m)	2.7	1.7	1.3	1.5	1.6
Euphotic zone depth (m)	7.3	5.6	4.4	4.9	5.1
Turbidity (NTU)	2.2	4.1	6.3	6.2	5.5
Hypolimnetic turbidity (NTU)	1.6	1.7	7.8	4.6	4.7
Conductivity (µS/cm)	19	24	25	26	24
Total dissolved solids (mg/L)	13	19	23	22	21
Dissolved oxygen (mg/L)	11.7	11.4	11.8	11.3	11.5
Hypolimnetic dissolved oxygen (mg/L)	9.3	10.1	10.7	11.5	10.8
pH	6.37	6.52	6.63	6.56	6.56
Total alkalinity (mg $CaCO_3$/L)	5.3	8.7	10.2	8.8	8.9
Dissolved inorganic C (µg/L)	2.68	3.73	4.11	3.64	3.72
Soluble reactive silica (mg Si/L)	0.14	0.48	0.53	0.46	0.46
Nitrate (µg N/L)	23.9	26.9	33.0	33.1	31.1
Hypolimnetic nitrate (µg N/L)	139.3	72.8	50.7	49.4	61.6
Ammonia (µg N/L)	3.8	3.4	4.6	6.5	5.1
Hypolimnetic ammonia (µg N/L)	8.6	4.2	3.6	5.6	5.0
Spring hypolimnetic total P (µg/L)	4.2	3.4	5.4	3.8	4.2
Spring hypolimnetic total dissolved P (µg/L)	4.5	3.0	4.0	3.7	3.7
Total P corrected for turbidity (µg/L)	4.1	5.0	9.4	6.1	6.7
Total dissolved P (µg/L)	2.3	3.5	6.0	4.7	4.6
Soluble reactive P (µg/L)	0.6	1.1	2.0	1.6	1.5
Particulate P (µg/L)	3.8	5.4	7.1	6.5	6.2
Bacteria (No.x10^6/mL)		0.74		0.84	0.51
Chlorophyll (µg/L)	1.01	1.50	1.18	0.98	1.15
Hypolimnetic chlorophyll (µg/L)	0.11	0.13	0.29	0.24	0.22
Photosynthetic rate (mg C·m²·day^{-1})	109	148	131	86	113
Picoplankton (<2 µm) (No.x10^3/mL)		1.38		13.50	12.55
Nanoplankton (2-20 µm) (No.x10^3/mL)		2.47		3.20	3.14
Microplankton (>20 µm) (No.x10^3/mL)		0.64		0.96	0.93
Particulate C:N:P molar ratio in May	256:18:1	157:14:1	127:14:1	186:18:1	168:11:1
Particulate C (µg/L) in May	223	182	143	126	150
Particulate N (µg/L) in May	18	20	18	14	17
Particulate P (µg/L) in May	2.25	3.00	2.90	1.75	2.37

Table 1 continued.

Variable	Station 1	2	3	4	Whole-lake average
Zooplankton number/m²					
Total	82,080	61,009	83,509	52,191	65,325
Daphnia	3,860	0	19	0	309
Acanthocyclops	13,025	2,340	4,978	1,790	3,700
Hesperodiaptomus	63,050	29,818	73,186	49,432	53,306
Ceriodaphnia	0	27,156	289	10	5,638
Bosmina	61	4	48	115	69
Zooplankton biomass (mg dry wt/m²)					
Total	384	251	367	207	276
Daphnia	74.7	0.0	0.3	0.0	6.0
Acanthocyclops	23.9	3.1	9.5	3.3	6.7
Hesperodiaptomus	284	223	355	203	257
Ceriodaphnia	0.0	24.0	0.3	<0.1	5.0
Bosmina	0.1	0.0	0.1	0.2	0.1

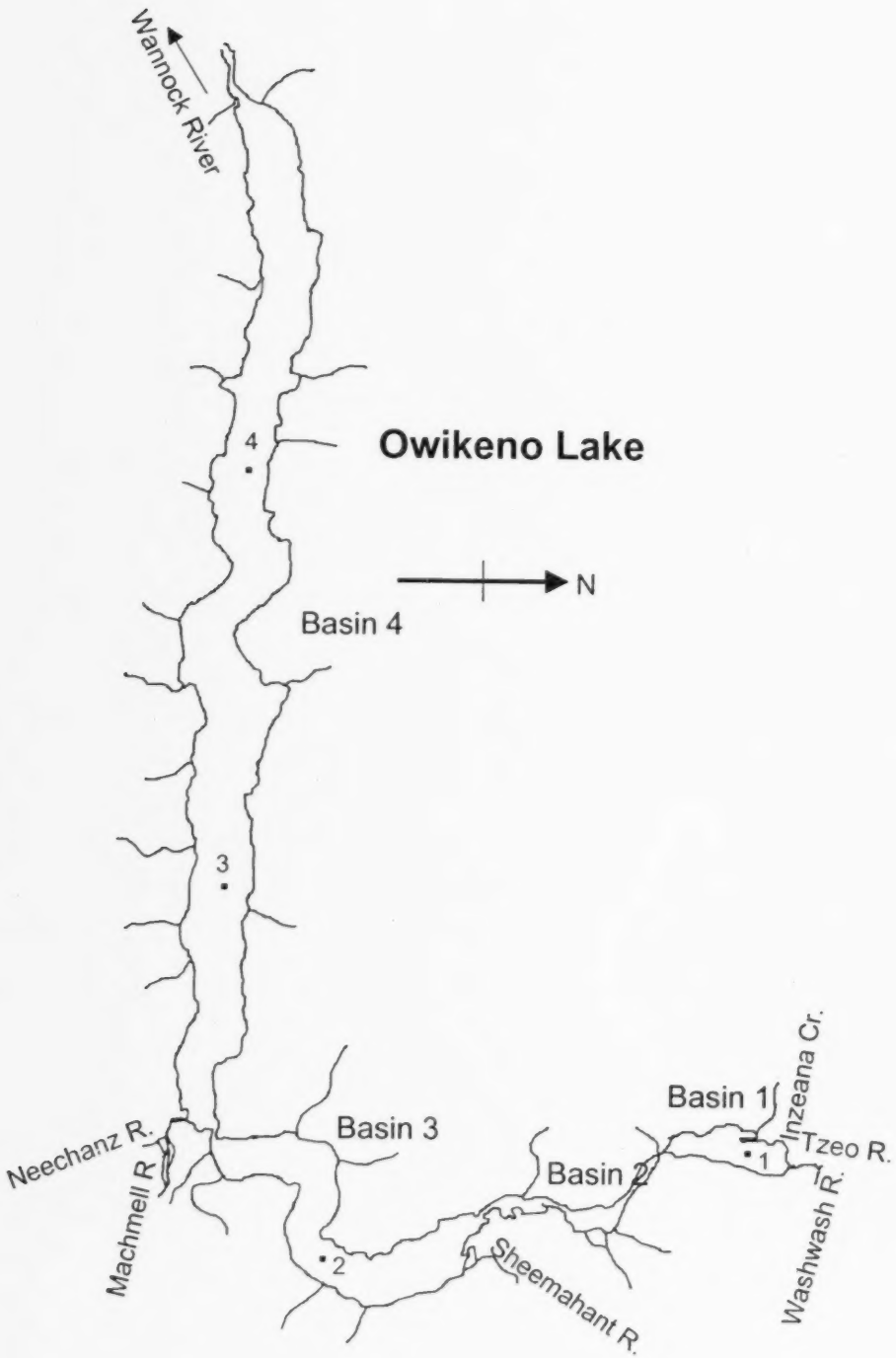

Fig. 1. Map of Owikeno Lake with location of the four sampling locations in the 2001 study.

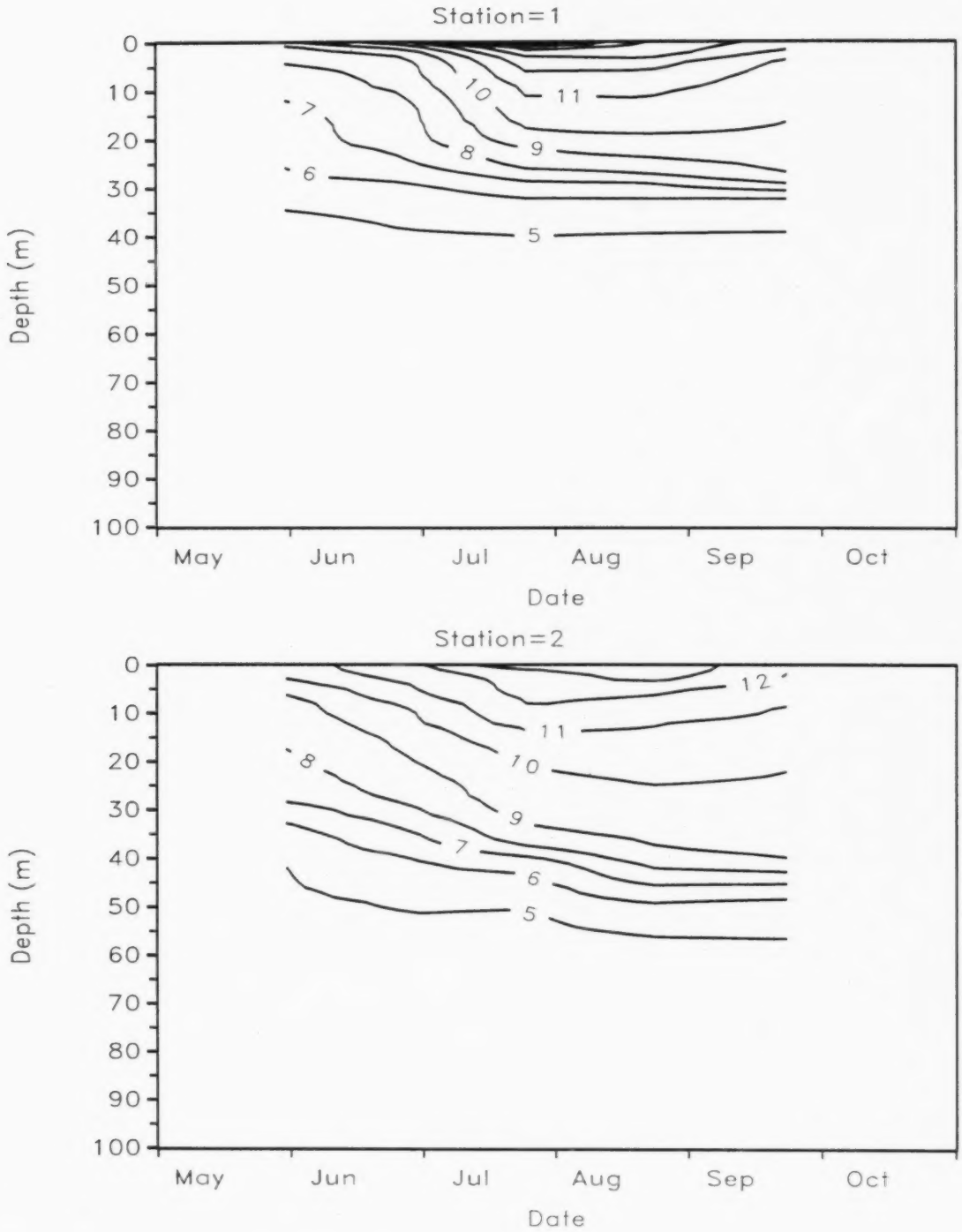

Fig. 2. Seasonal temperature isolines at stations 1 and 2 in 2001.

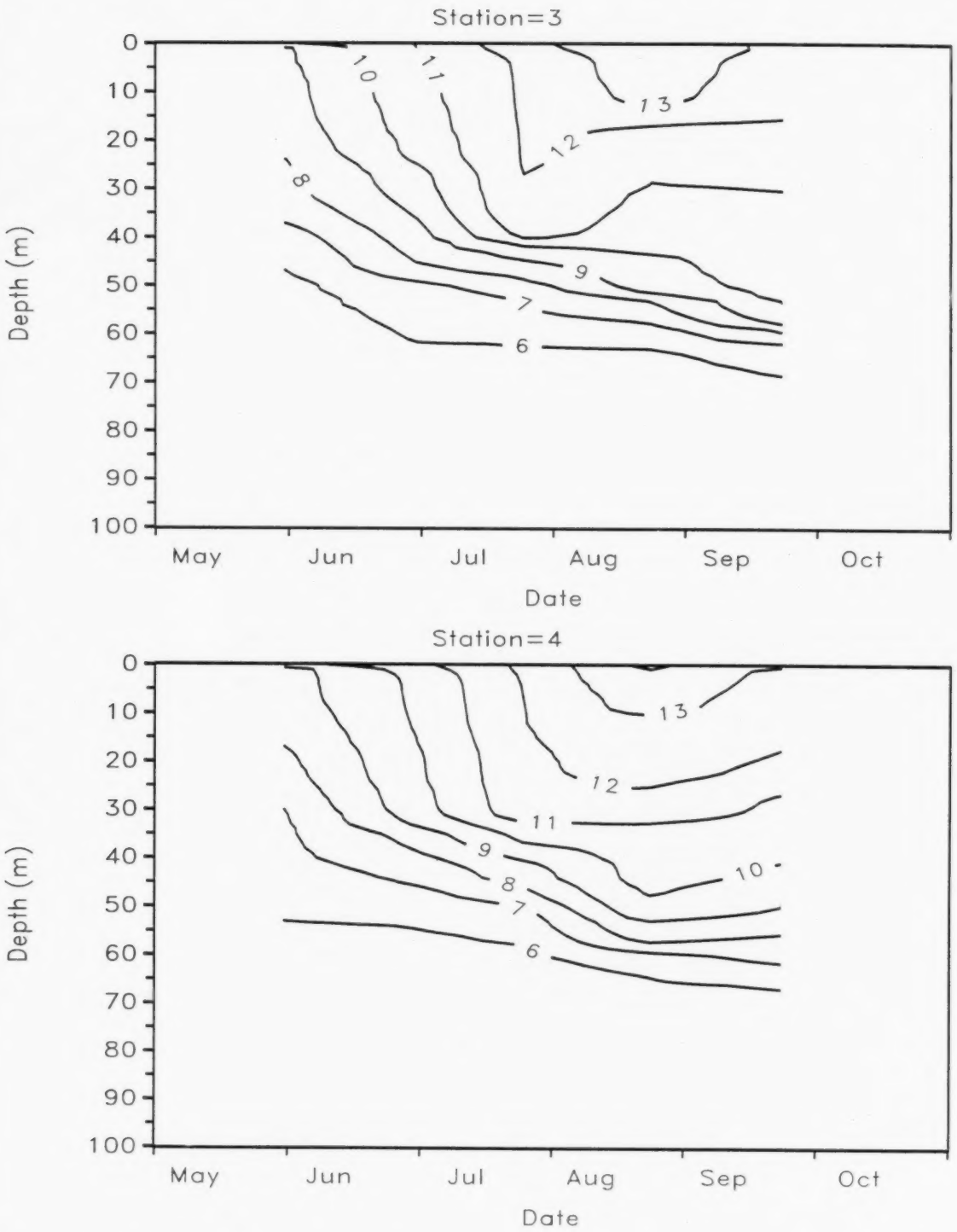

Fig. 3. Seasonal temperature isolines at stations 3 and 4 in 2001.

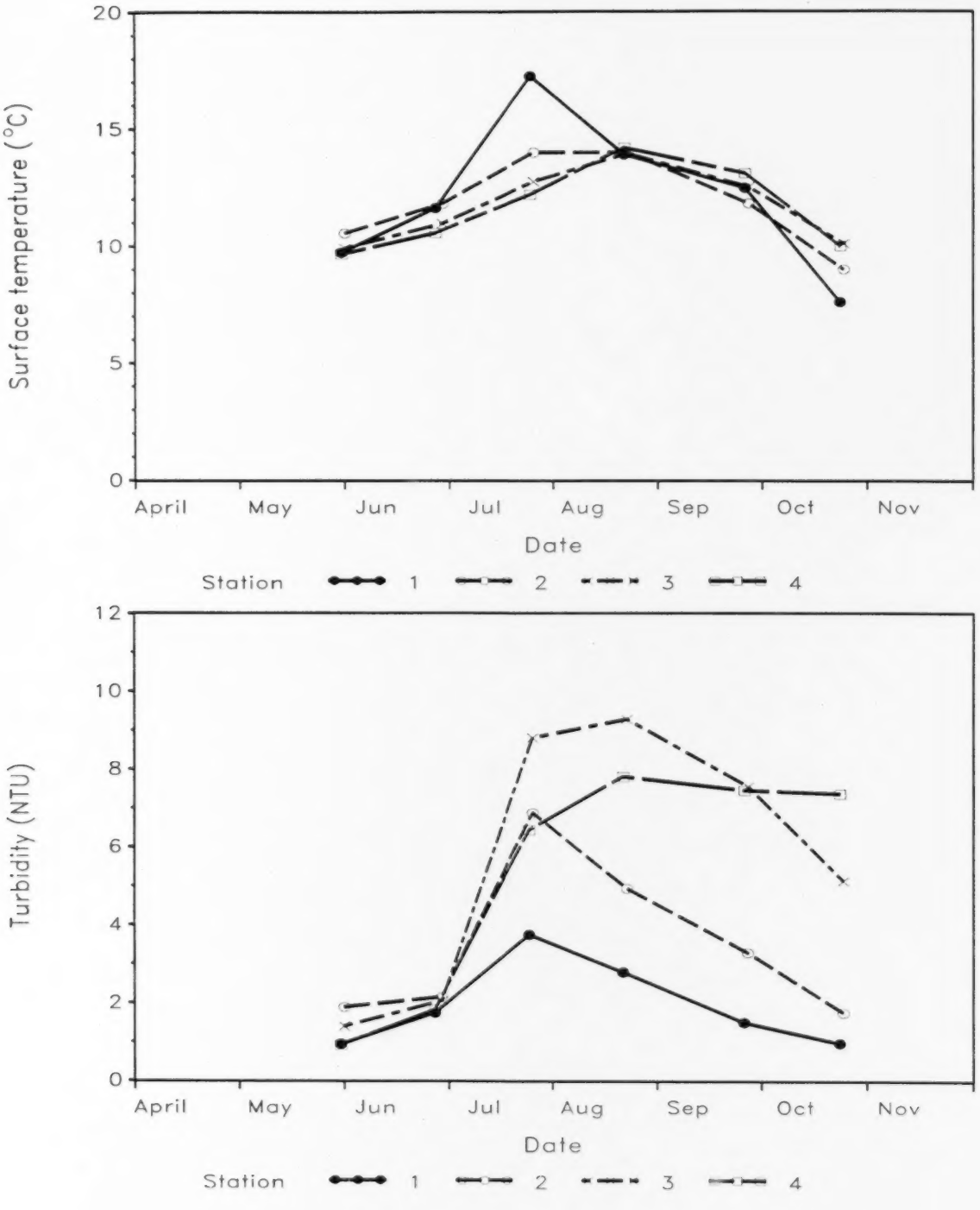

Fig. 4. Seasonal variation in surface temperature and turbidity (NTU) in the euphotic zone in 2001.

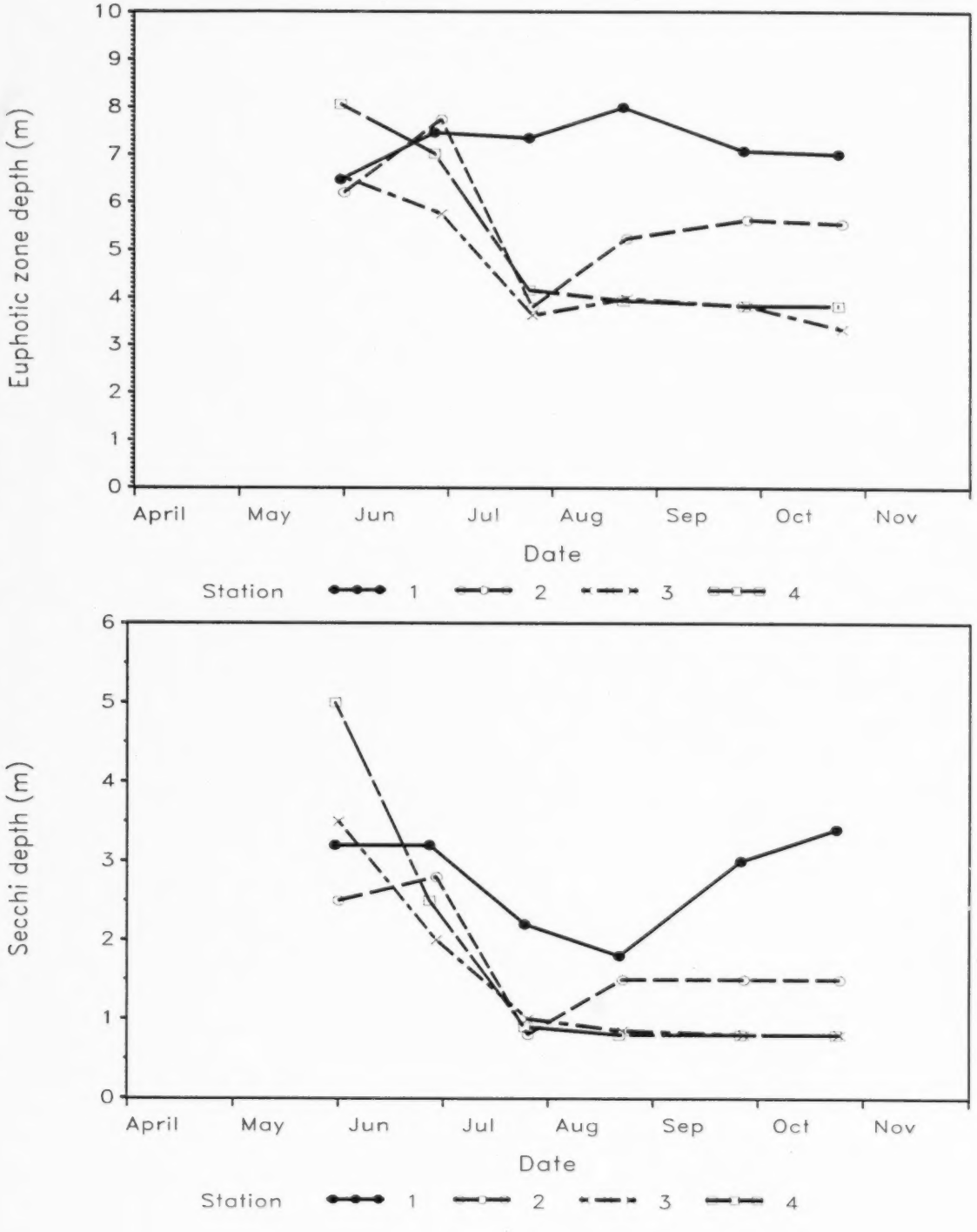

Fig. 5. Seasonal variation in euphotic zone depth and Secchi depth in 2001.

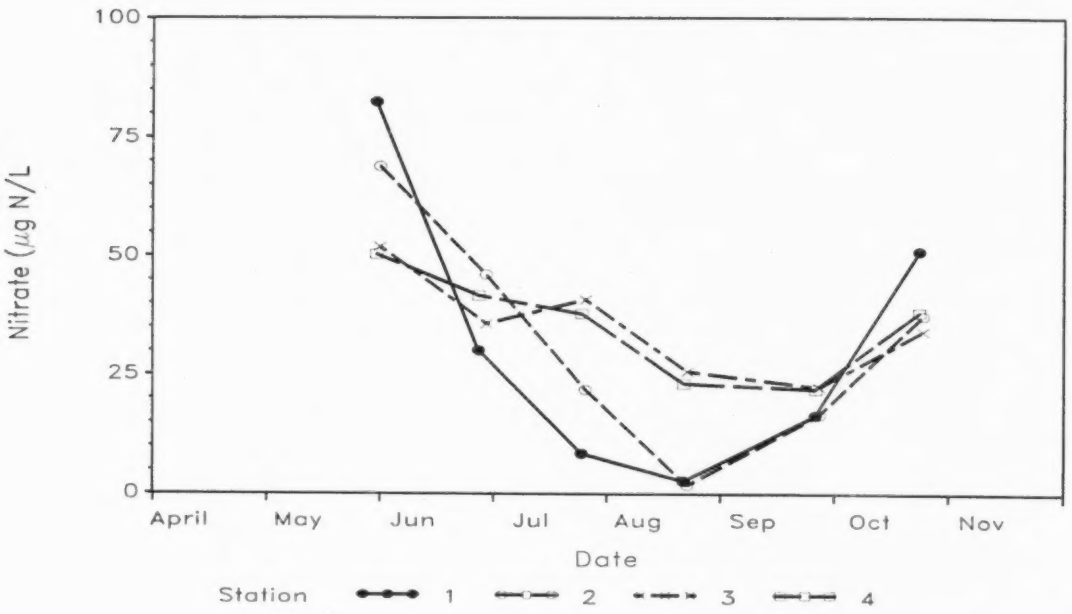

Fig. 6. Seasonal variation in nitrate concentration in the euphotic zone at stations 1-4.

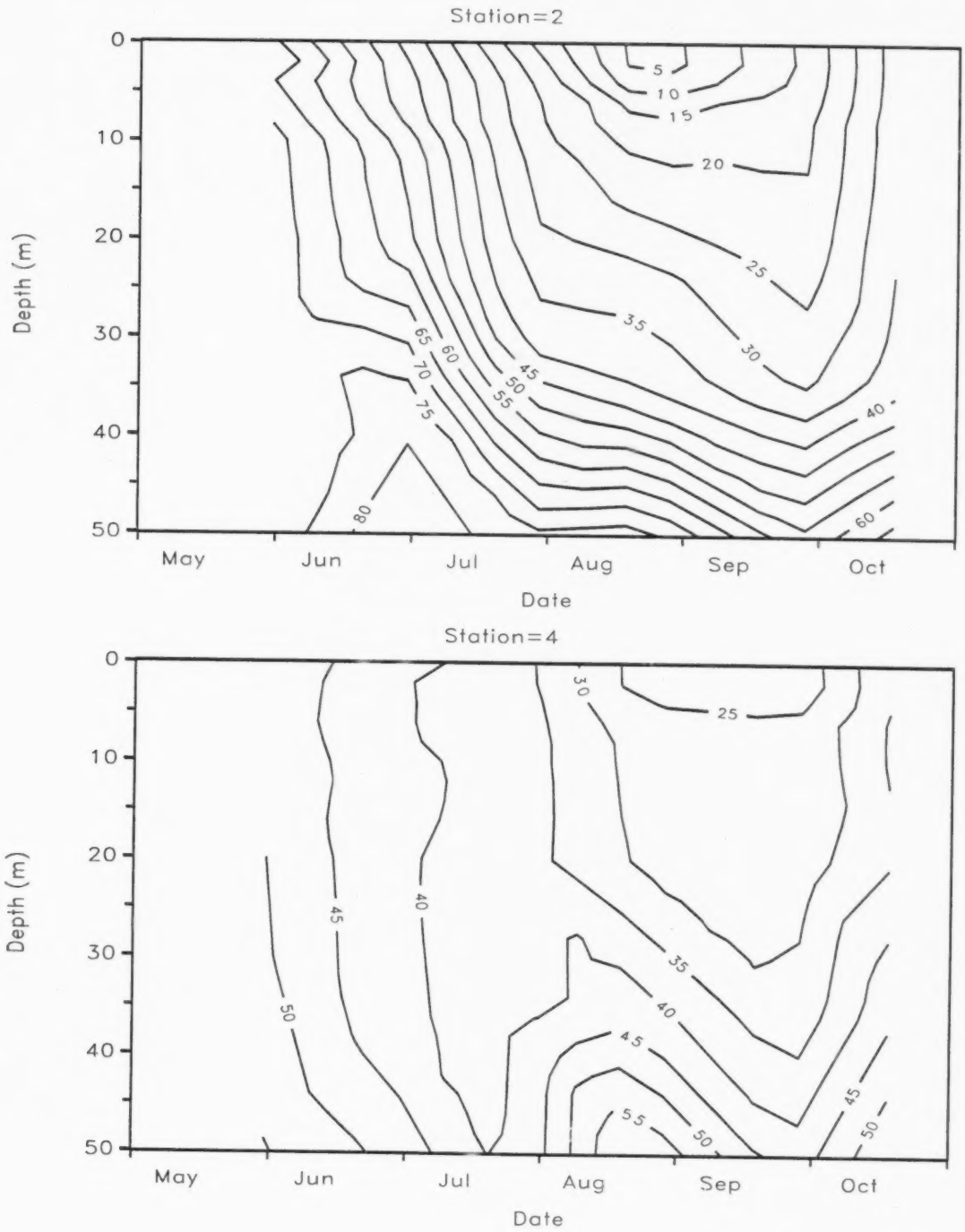

Fig. 7. Seasonal isolines of nitrate concentration (µg N/L) and stations 2 and 4 in 2001.

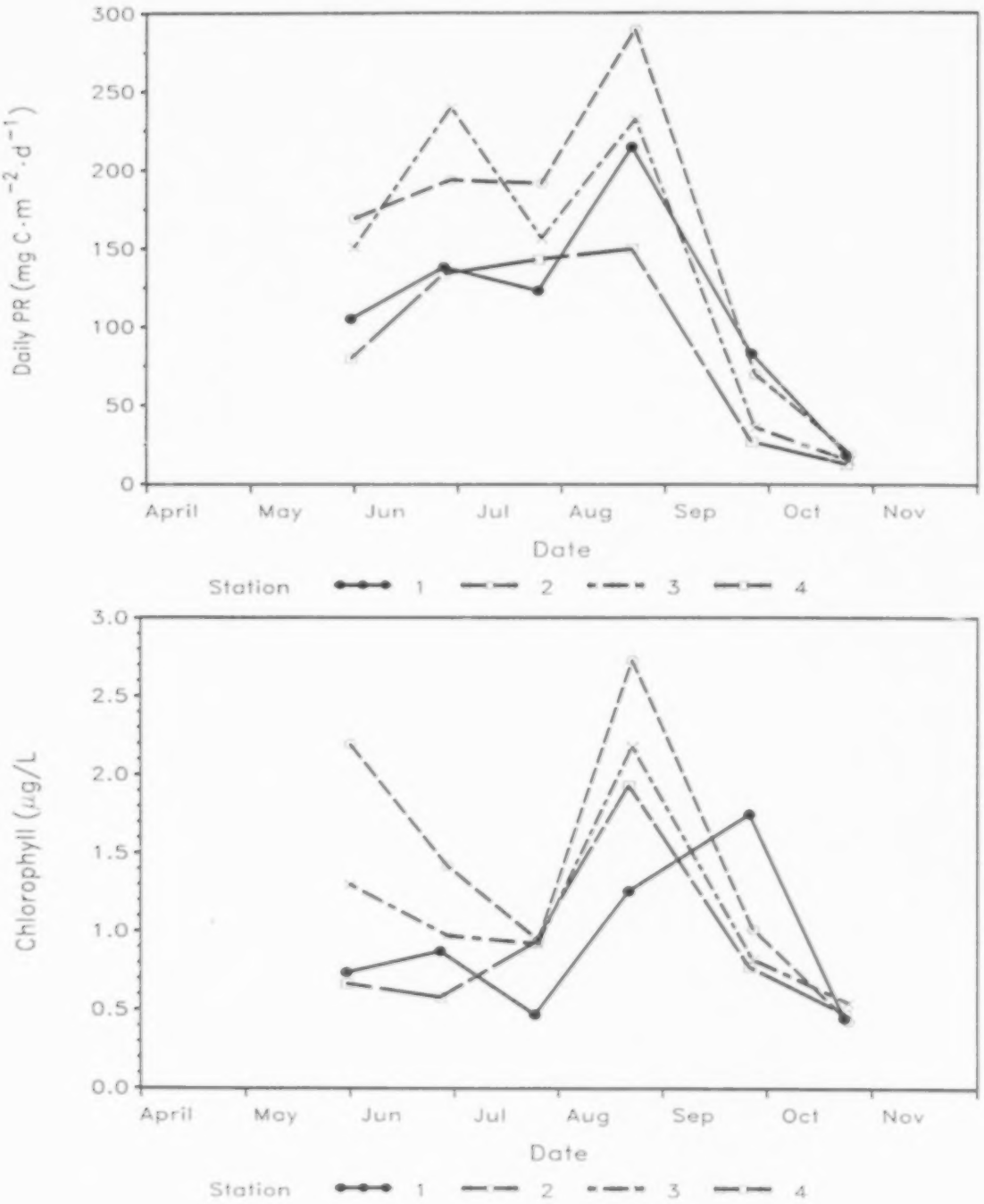

Fig. 8. Seasonal variation in photosynthetic rate and in average chlorophyll concentration in the euphotic zone in 2001.

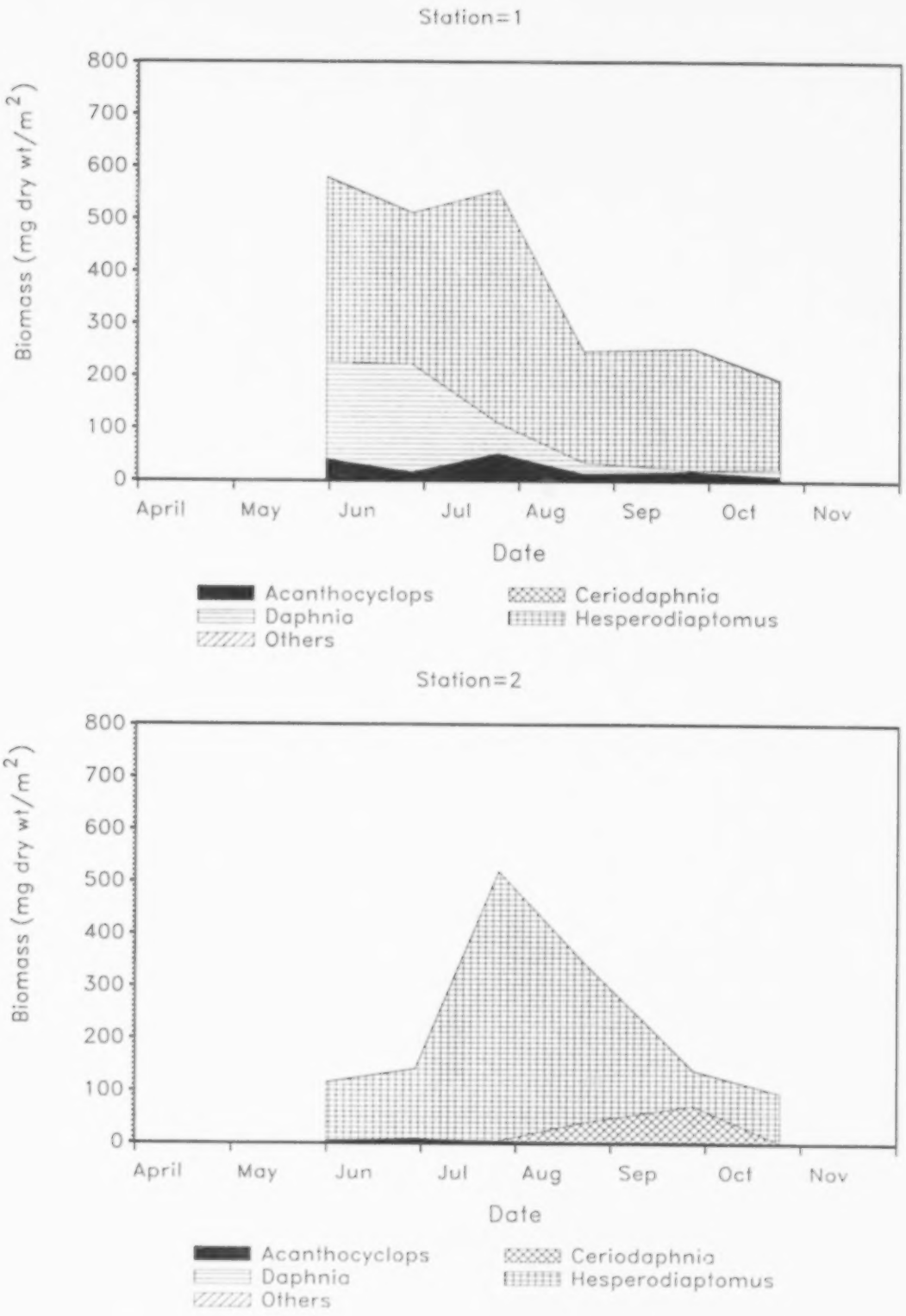

Fig 9. Seasonal variation in biomass of major zooplankton genera at stations 1 and 2 in 2001.

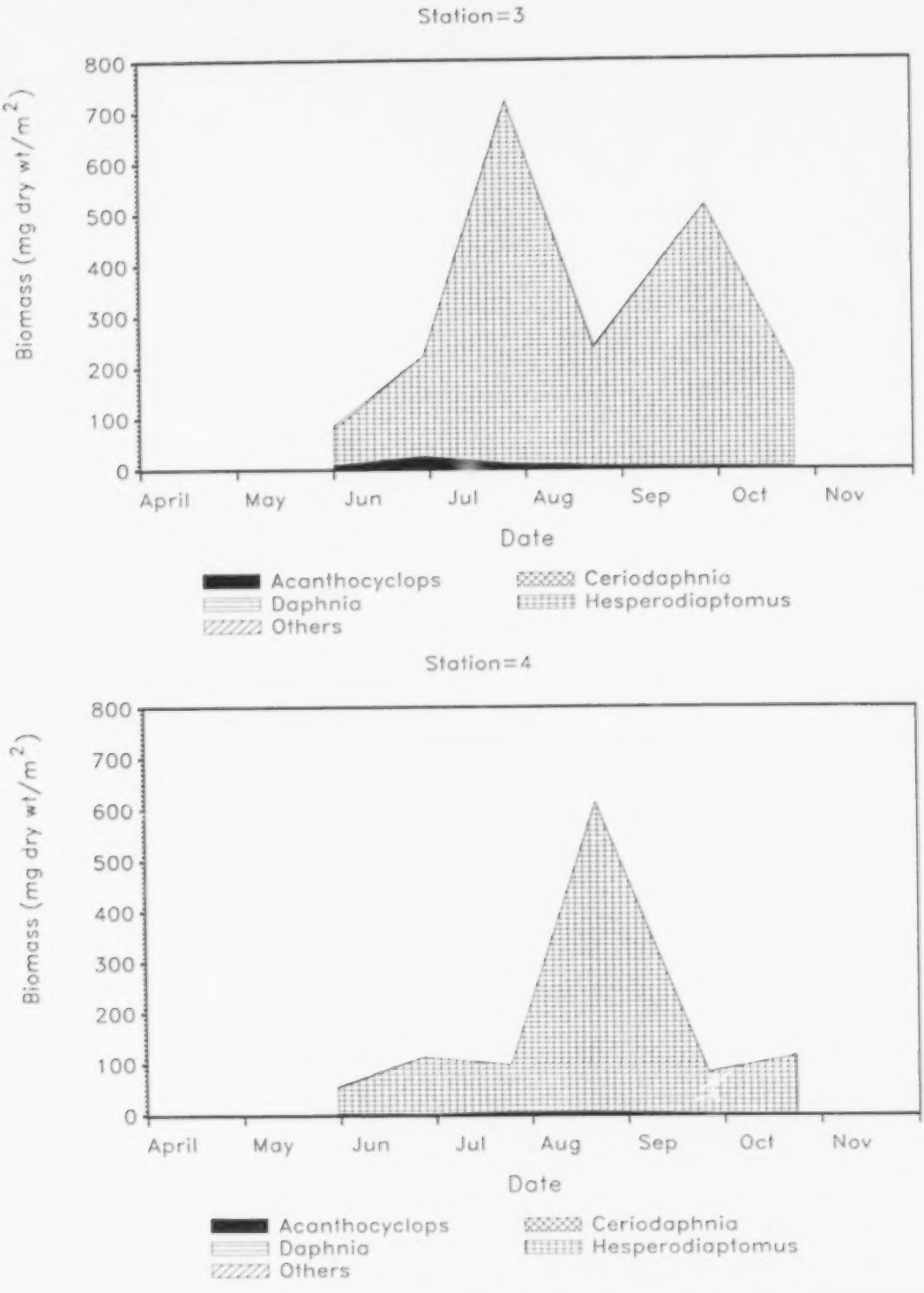

Fig. 10. Seasonal variation in biomass of major zooplankton genera at stations 3 and 4 in 2001.

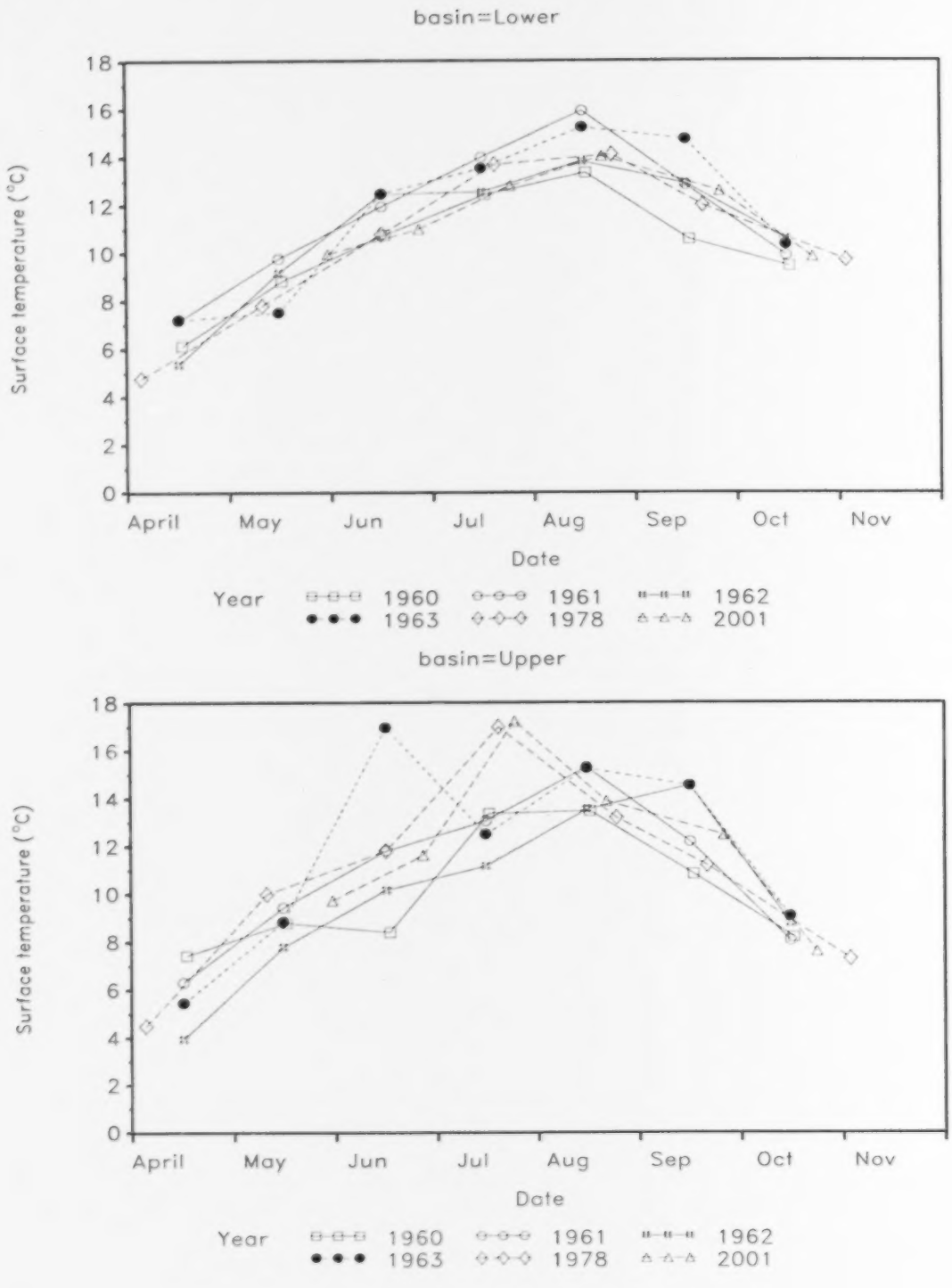

Fig. 11. Seasonal variation in surface temperature in the upper (basin 1) and lower (combined basins 3 and 4) basins of Owikeno Lake in the 1960's, 1970's, and in 2001.

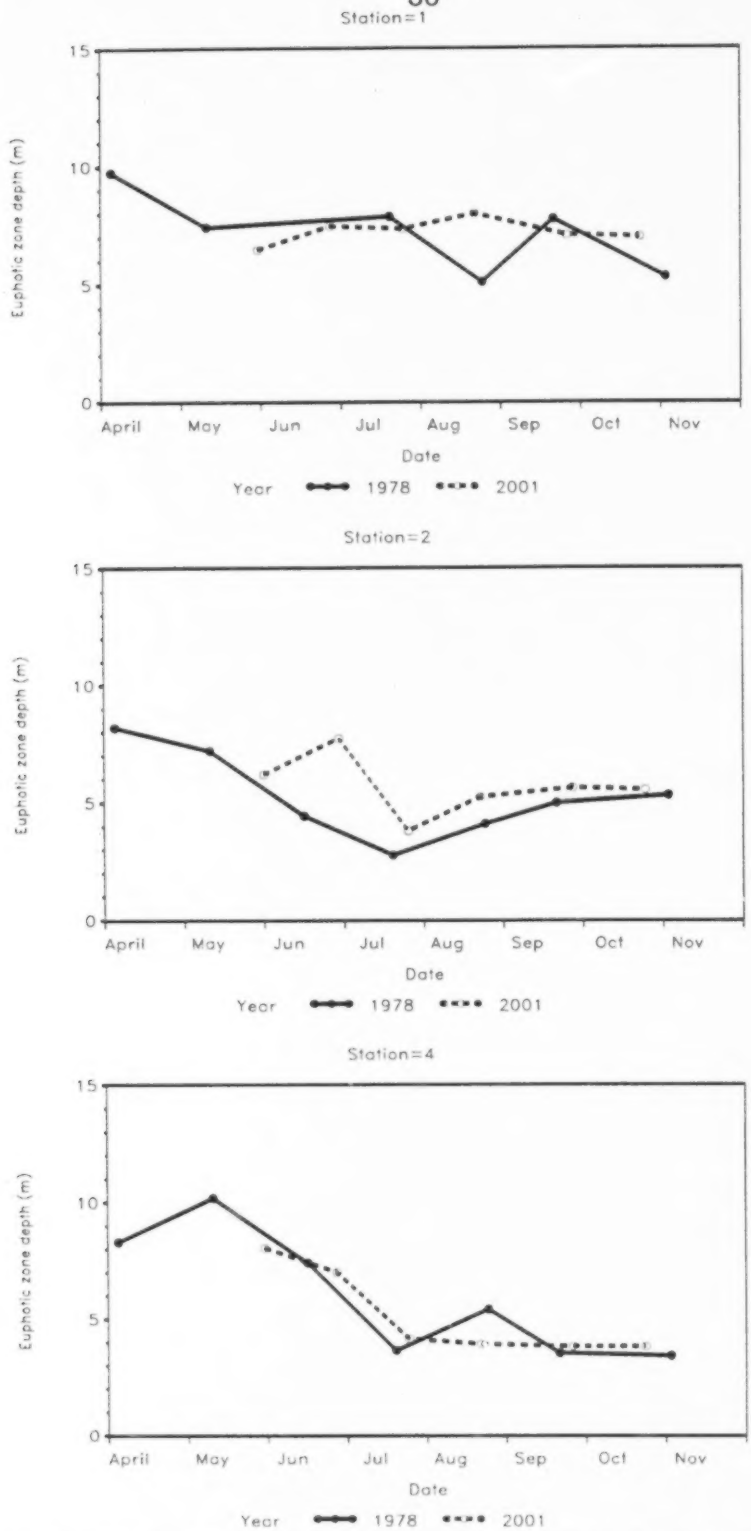

Fig. 12. Seasonal variation in euphotic zone depth at stations 1, 2, and 4 in 1978 and in 2001.

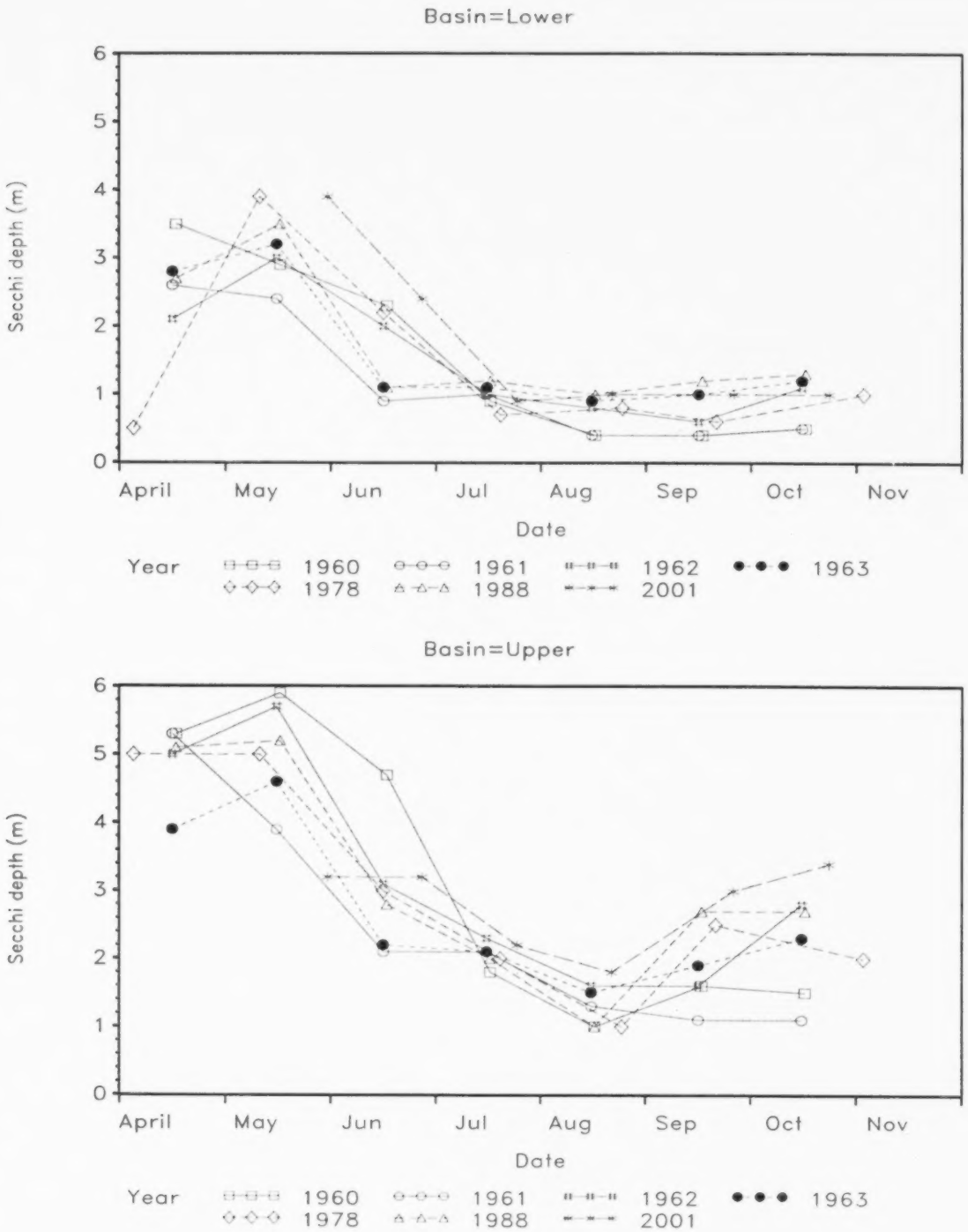

Fig. 13. Seasonal variation in Secchi depth in the upper (basin 1) and lower (combined basins 3 and 4) basins of Owikeno Lake in the 1960's, 1970's, 1980's, and in 2001.

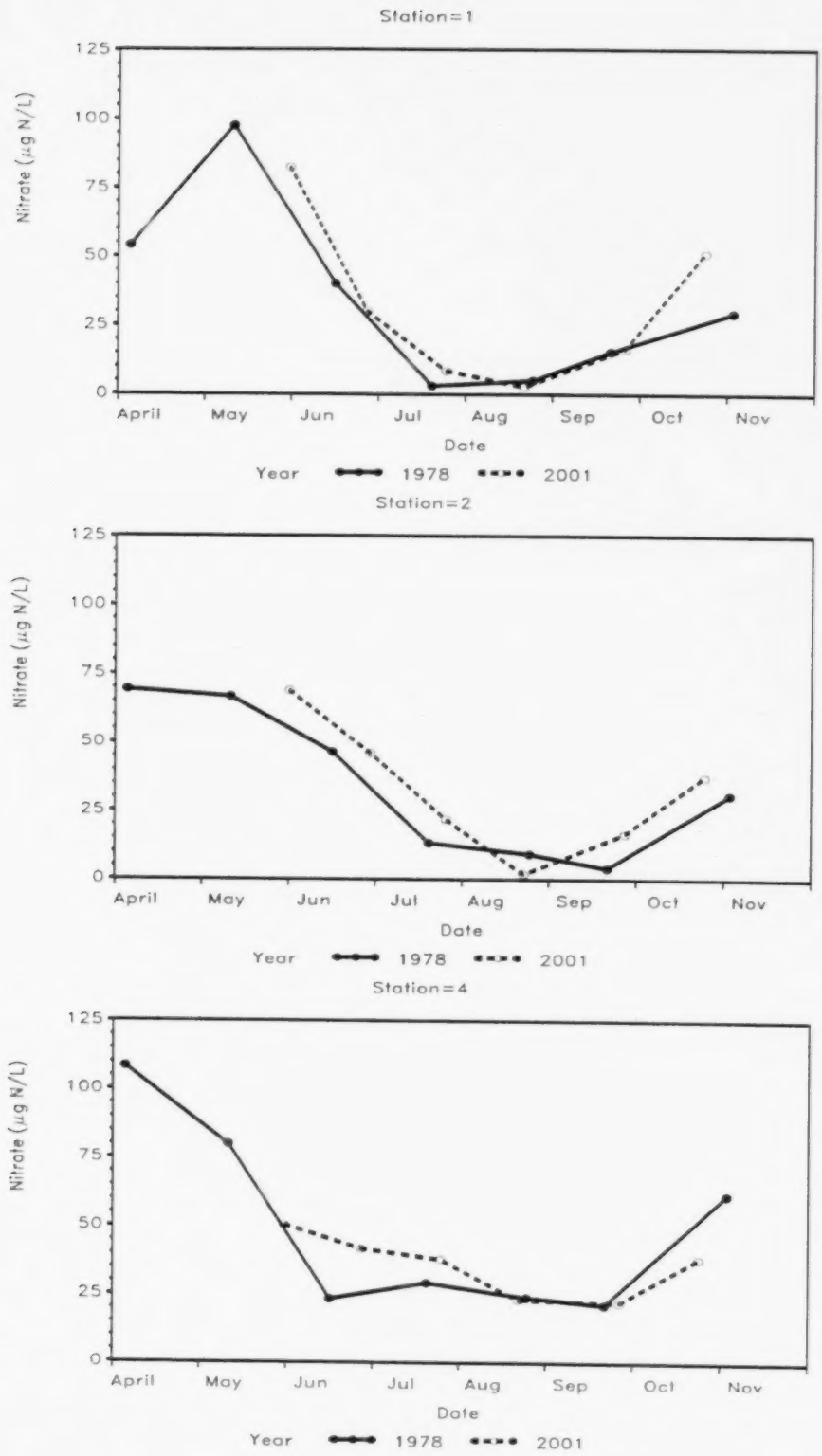

Fig. 14. Seasonal variation in nitrate concentration at stations 1, 2, and 4 in 1978 and in 2001.

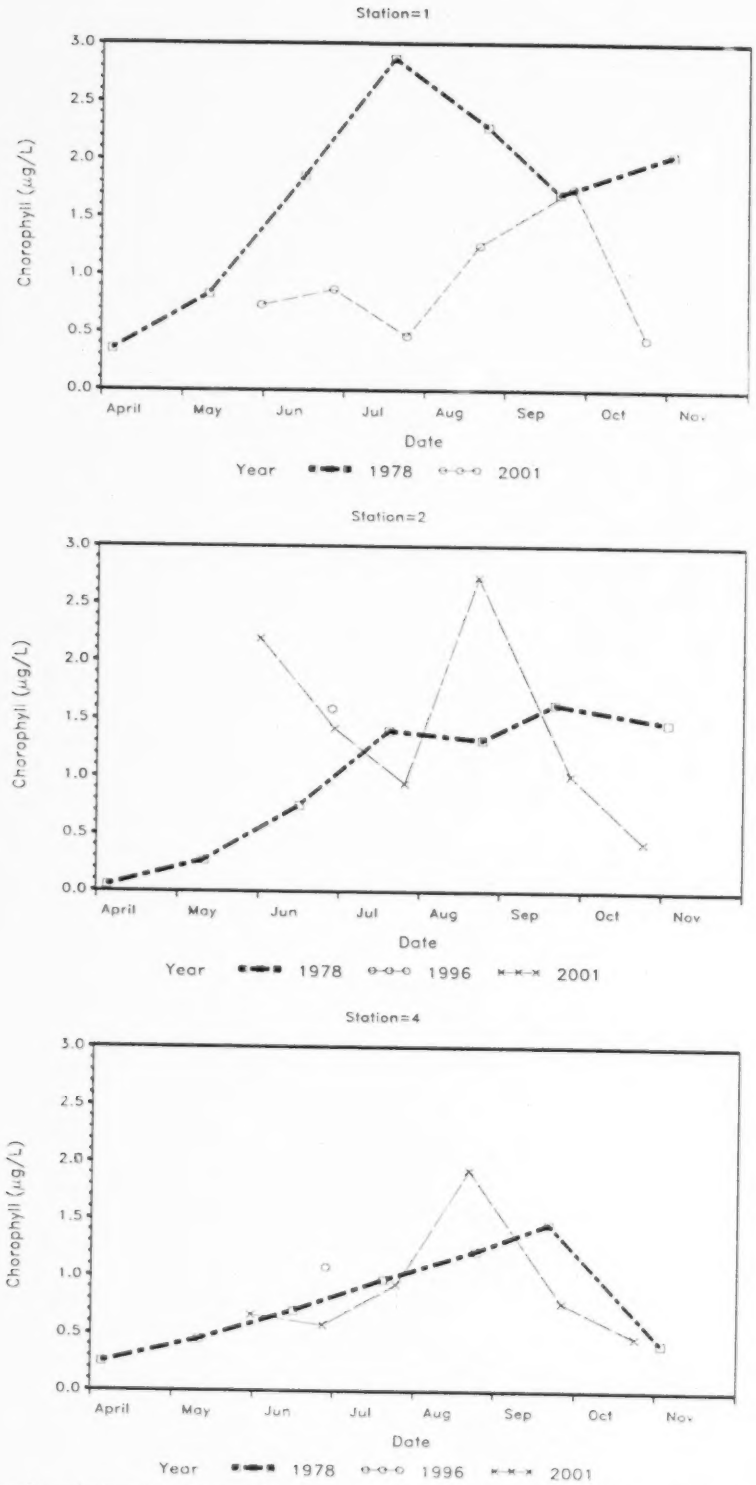

Fig. 15. Seasonal variation in chlorophyll concentration at stations 1, 2, and 4 in 1978, on one date in 1996, and in 2001.

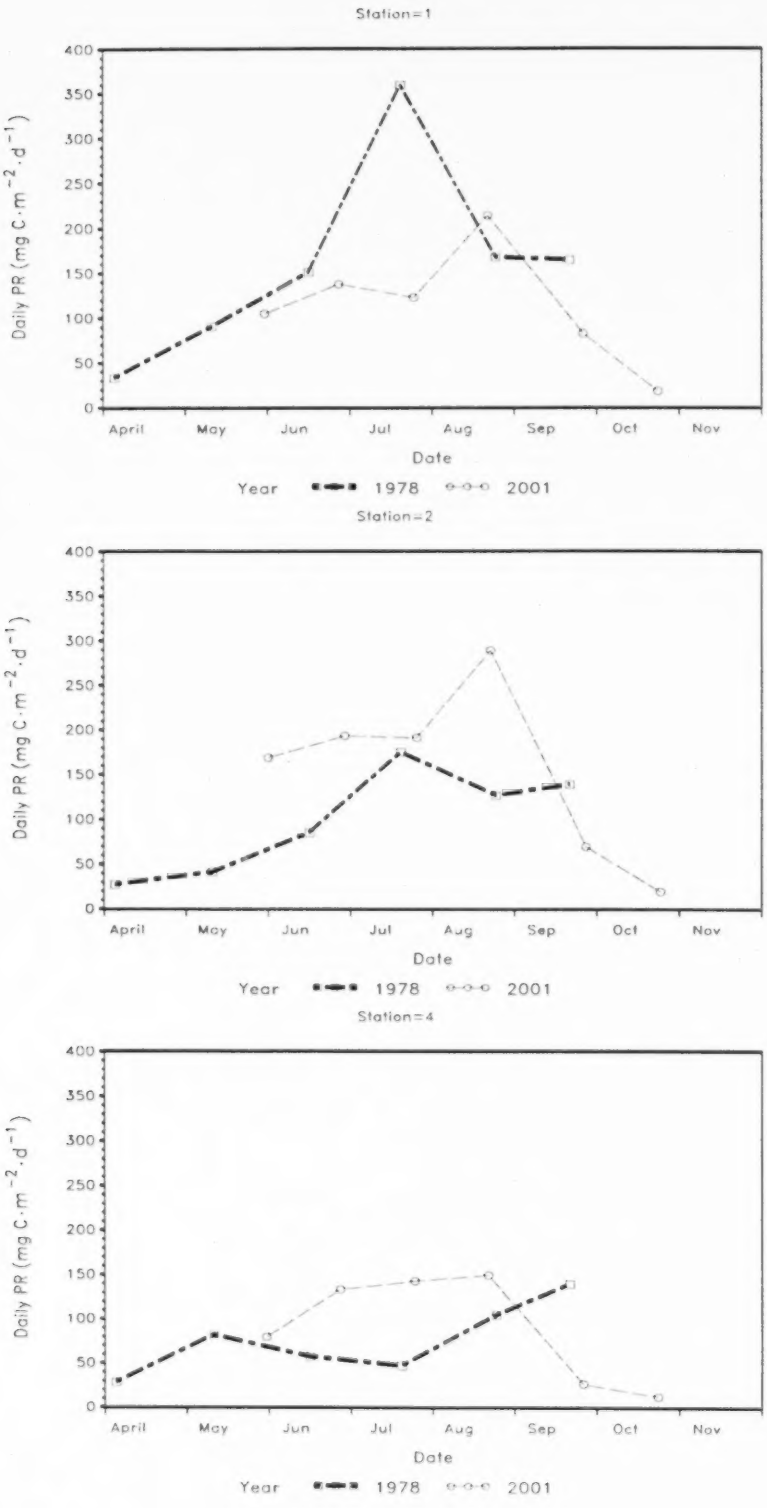

Fig. 16. Seasonal variation in photosynthetic rates at stations 1, 2, and 4 in 1978 and in 2001.

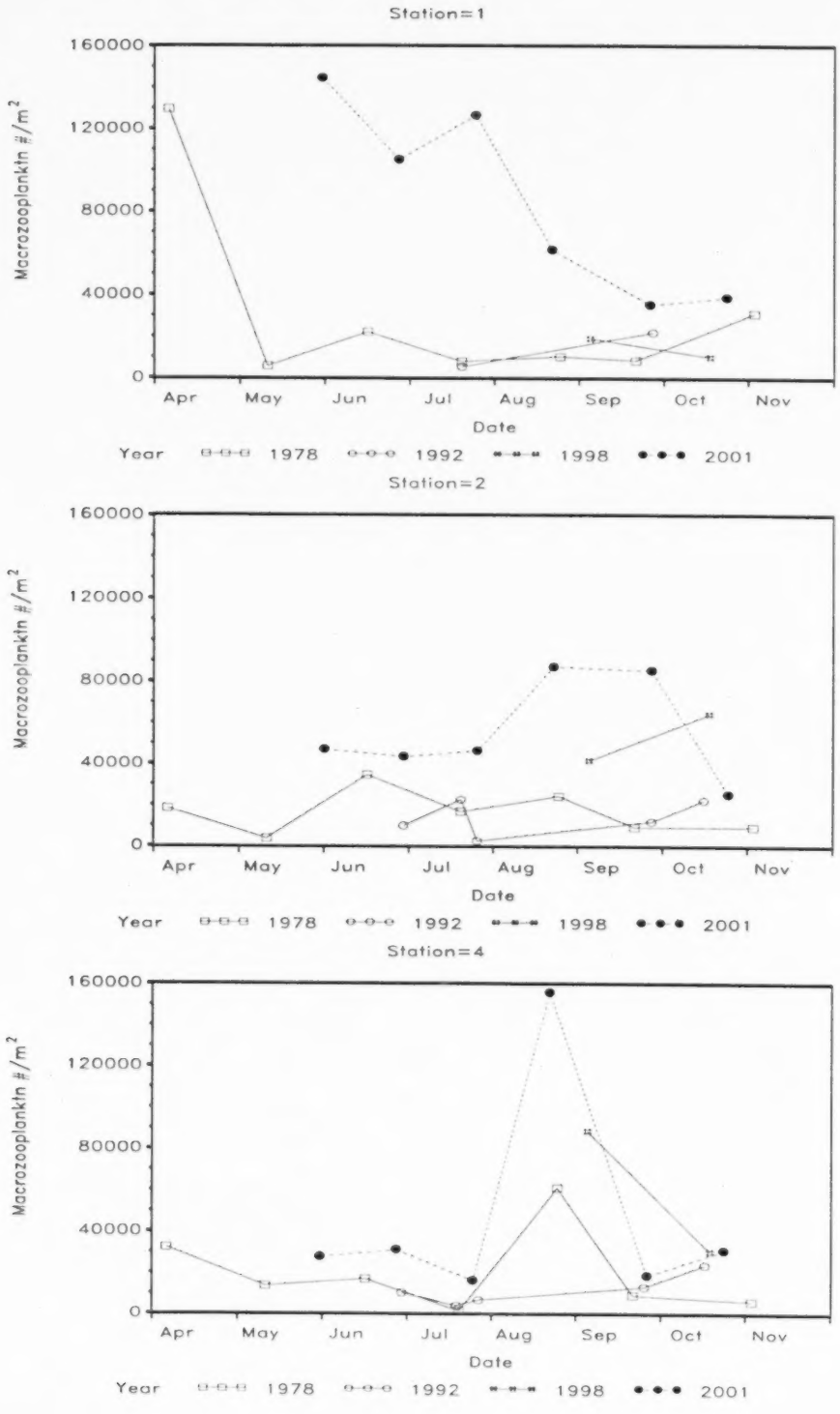

Fig. 17. Seasonal variation in zooplankton numbers at stations 1, 2, and 4 in 1978, in the 1990's, and in 2001.

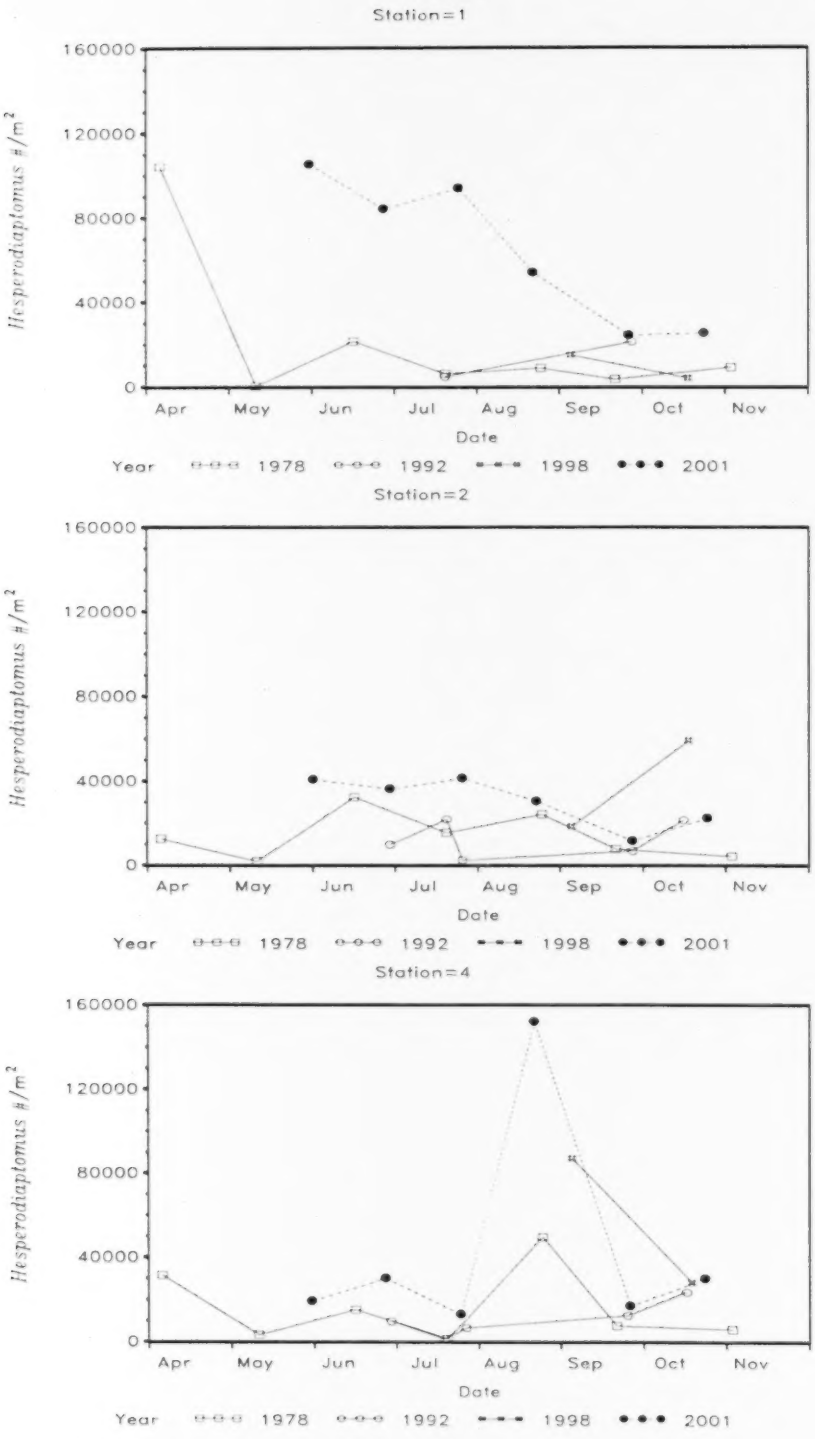

Fig. 18. Seasonal variation in numbers of *Hesperodiaptomus* in 1978, in the 1990's, and in 2001.